STUDIES GENETICAL AND PHYSIOLOGICAL UPON THE POTATO. (SOLANUM TUBEROSUM).

THESIS

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C O N T E N T S.

GENERAL INTRODUCTION

The investigations to be described have been undertaken throughout at the Scottish Plant-Breeding Station, Corstorphine, Edinburgh, under a special scheme for research into the virus diseases of the potato. An enquiry into the effects of virus diseases upon the metabolism of potatoes has been followed as a particular line of study under this scheme and the earlier results of investigation have already been published in a series of papers by BARTON WRIGHT and McBAIN (1932, 1933 (a), 1933 (b)) and COCKERHAM (1933) under the general title "Studies in the Physiology of the Virus Diseases of the Potato." These publications relate to the effects upon carbohydrate metabolism of the leaf roll virus, the crinkle complex and the "para-crinkle" virus in a "carrier" variety and to the effects of the leaf roll virus upon nitrogen metabolism. A cognate investigation into the metabolism of potato plants affected with a mild mosaic disease has also been followed and the details of this latter study are brought together in Section 1 of this thesis.

The further investigations, presented in Sections/

Sections 2 and 3, have been based upon the broad plan of research given in detail below.

1. To inbreed plants affected with virus diseases in a non-infected area in order to determine if the diseases are transmitted through the seed.

2. To select, as eventual parents of resistant strains, proved and tested plants of varieties which are at the present time reputed to be amongst the most resistant to virus diseases in ordinary agricultural practice.

3. To inbreed and/or hybridise suitably these selected plants and to test the progenies under conditions in which infection by virus diseases may readily occur.

4. To determine whether Mendelian segregation occurs as regards susceptibility to virus diseases.

5. To continue breeding from those seedlings found to be most resistant to virus diseases, through a number of generations, with repeated tests for resistance under various environmental conditions.

6. To compare the morphological, physiological and biochemical characteristics of the various progenies; these characters to be determined as far as possible for healthy specimens of susceptible and resistant seedlings, the object being to obtain an insight into the real nature of resistance and susceptibility.

The essential problems outlined in this plan may be more generally stated to be concerned firstly/

firstly with the effects of virus diseases on the reproductive qualities of the potato and secondly with the genetical and physiological aspects of resistance and susceptibility to virus diseases. A preliminary examination of the first of these problems was initiated in 1930 at the North of Scotland sub-Station of the Scottish Society for Research in Plant-Breeding. During the course of this investigation it was established that in the potato viruses are not transmitted through the sexually formed seed. Nevertheless, sufficient indication of abnormal reproduction in diseased plants was obtained to merit further study. The scope of the work was extended, therefore, to include examination of this new problem and the progressive results of the extended investigation have been described briefly in the Annual Report of the Scottish Society for Research in Plant-Breeding for the years 1931-1935. In these Reports it has been stated that reproduction is affected in two directions. The reproductive capacity of the parent varieties was found to be considerably reduced and the progenies raised from diseased parents were found to contain abnormal, but virus-free, seedlings. The causation of these abnormal types, which were previously undescribed and quite distinct from the hereditary degenerate types occurring/

occurring in many progenies, has been sought in physiological disturbances brought about by the disturbed metabolism of the parent varieties. One of the chief factors affecting reproduction directly was observed in a reduction of the flowering capacity of normal free-flowering varieties after infection with virus diseases and evidence accrued to indicate that the reduction was differential with regard to both the diseases concerned and the nature in which it was brought about. When, therefore, facilities became available at the Plant Breeding Station in 1936 opportunity was taken to examine in greater detail the effects of virus infection upon reproduction and vigour and to place the results upon a statistical basis. This investigation is reported in Section 2.

The second basic problem arising out of the general plan of research has been stated to concern the genetical and physiological aspects of resistance and susceptibility to virus diseases of the potato. Work upon the lines indicated in paragraphs 2-6 of the general plan was commenced in 1935 and the data obtained have been presented in Section 3 as a preliminary and experimental survey of the possibility that resistance to virus diseases is inherent within the cultivated varieties of the potato/

potato and is, moreover, of a heritable nature.

The fact that aphides are the normal vectors of three of the common viruses of the potato suggests at once that the distribution and the ecological relationships of these insects are factors of outstanding importance in any investigation dependent upon the spread of virus diseases under natural conditions. The field studies upon resistance to virus diseases are dependent upon such spread and it was considered essential, therefore, to make a preliminary seasonal survey of the aphis populations in each of the environments in which the various trials were conducted. The details of this survey and of its extensions are presented briefly in Section 4.

PUBLICATIONS CITED

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SECTION I

Part 1

A Comparison of the Metabolism of Mosaic Infected Potatoes with that of Normal Potatoes.

I. The Carbohydrate Metabolism of the Normal Leaf.

C O N T E N T S

INTRODUCTION

The effects of mosaic viruses upon the metabolism of the host plant have been judged chiefly upon data derived from chemical analyses of plants or plant organs and from respiration studies upon detached leaves. The former of these methods of approach suffers from the disadvantage that the information provided often refers only to samples unique or widely separated in time and consequently throws but little light upon the cause and nature of the disturbances which give rise to the observed effects. Respiration studies, on the other hand, although expressive of the continuity essential in a consideration of metabolism, examine only one aspect of the complex changes involved. It would seem then that a wider estimate of the effects of mosaic viruses upon the biochemical relationships of the host plant could best be obtained by a comparative study of normal and mosaic infected plants in relation to the continuity of metabolic change.

An investigation designed to examine the various aspects of carbohydrate, nitrogen and mineral metabolism of normal and diseased plants was contemplated but practical and administrative difficulties/

difficulties arose to restrict the scope of the work. A considerable amount of data upon diurnal and seasonal variations in the three principle carbohydrates and the total nitrogen fractions of the leaf had been obtained before the restrictions became effective, however, and these are presented and discussed in the following pages.

The investigation has provided results which controvert, in part, and extend those previously published upon the nature of carbohydrate metabolism in potato leaves, (DAVIS and SAWYER [1916], CLEMENTS [1930] and BARTON WRIGHT and McBAIN [1932,1933]), and it is most convenient, therefore, to present and examine firstly those data obtained from the healthy material. The findings of this examination will serve subsequently as a basis upon which to establish a comparison between the metabolism of mosaic infected leaves and that of normal leaves.

MATERIAL

The potato varieties used throughout this investigation were President and Arran Victory. Sixty plants of each variety were grown under greenhouse conditions at Huntly, Aberdeenshire, and comparable conditions were maintained between individuals within each variety by equality of treatment and by frequent change of position of the plants with regard to favourable and unfavourable bench positions. Random samples, from the intermediate regions of the stem, consisting of 20 whole leaves were taken at intervals of two hours over each of the diurnal periods to be considered.

The first batch of samples from President was obtained when the plants were 20 days old, age being reckoned from the first appearance of shoots at soil level. At this stage of growth the shoots were 6-10 inches in height and bore only five or six developing leaves none of which, however, was fully expanded. In consequence of the severe injury which these young plants suffered by sampling they were discarded and the subsequent diurnal samples together with the seasonal samples were obtained from a parallel group of 60 plants raised under the same conditions. These latter diurnal samples/

samples from President and the two samplings from Arran Victory were made upon plants which had reached a vigorous vegetative stage of growth just prior to flowering and again after flowering when vegetative growth had almost, if not completely, ceased. In the case of Arran Victory the samples were taken when the plants were 30 and 72 days old respectively and in the case of President at 44 and 86 days from the appearance of shoots at soil level. The data to be presented are thus representative of early vegetative, pre-flowering and post-flowering stages of growth and refer to leaves which, except in the case of President Series 1, were fully expanded at the time of sampling.

An estimate of the seasonal variations in total carbohydrates was obtained from samples of 20 leaves removed at weekly intervals from the plants used in the diurnal experiments. Each weekly sample from Arran Victory was obtained at 10 a.m. G.M.T. and those from President at 11.0 a.m. G.M.T.

METHODS

The treatment of the samples in preparation for analysis was similar to that used by BARTON WRIGHT and McBAIN (1933). Immediately after collection the petiole of each leaf was severed at the lower extremity of the leaf-blade after which the midrib and main veins were removed from the lamina and discarded. The petioles and laminae were subsequently treated as separate units. Each unit was finely divided and placed in a wide-mouthed beaker-flask to which a few drops of ammoniated xylol were added. Drying was carried out in two stages, firstly at a temperature of 90°-95° C. and finally, to constant weight, at 60°-65° C. as recommended by LINK and TOTTINGHAM (1923).

When required for analysis weighed portions of redried and finely ground material were extracted in distilled water for 24 hours. The extract after filtration was cleared by boiling with colloidal ferric hydroxide in the manner described by THOMAS (1927), refiltered and made up to volume. Reducing sugars were estimated directly upon the cleared plant extract and disaccharides were determined upon duplicate aliquots of which one was/

was inverted with 2.5% hydrochloric acid and the other with a 0.5% solution of invertase buffered to pH 4.7. The duplicated results were in almost perfect agreement and the mean values, expressed as sucrose, were used in subsequent calculations.

The residue after extraction was taken up in distilled water, boiled and then cooled, after which it was incubated at 30° C for 24 hours with a ptyalin solution buffered to pH 6.7 and filtered. The filtrate was further hydrolysed with 2% sulphuric acid by boiling on a water bath for 1 hour. The hydrolysed filtrate was then exactly neutralised with 40% caustic soda, made up to volume and starch estimated as reducing sugars in which form the values are expressed in the curves and tables. The carbohydrate analyses throughout were effected by the SCHAFFER-HARTMANN (1921) microtechnique.

Estimates of the total carbohydrates in the seasonal samples were obtained after preliminary hydrolysis of the finely ground dried material with 2.5% sulphuric acid.

All calculations have been based upon the residual dry weight as proposed by MASON and MASKELL (1928) and the standard error has been attached to each calculated mean value. In order to express/

express more clearly the seasonal differences in carbohydrate relationships the data for each diurnal sample have also been calculated as percentages of the total estimated carbohydrates and subjected to statistical treatment of the same form as that given to the actual values.

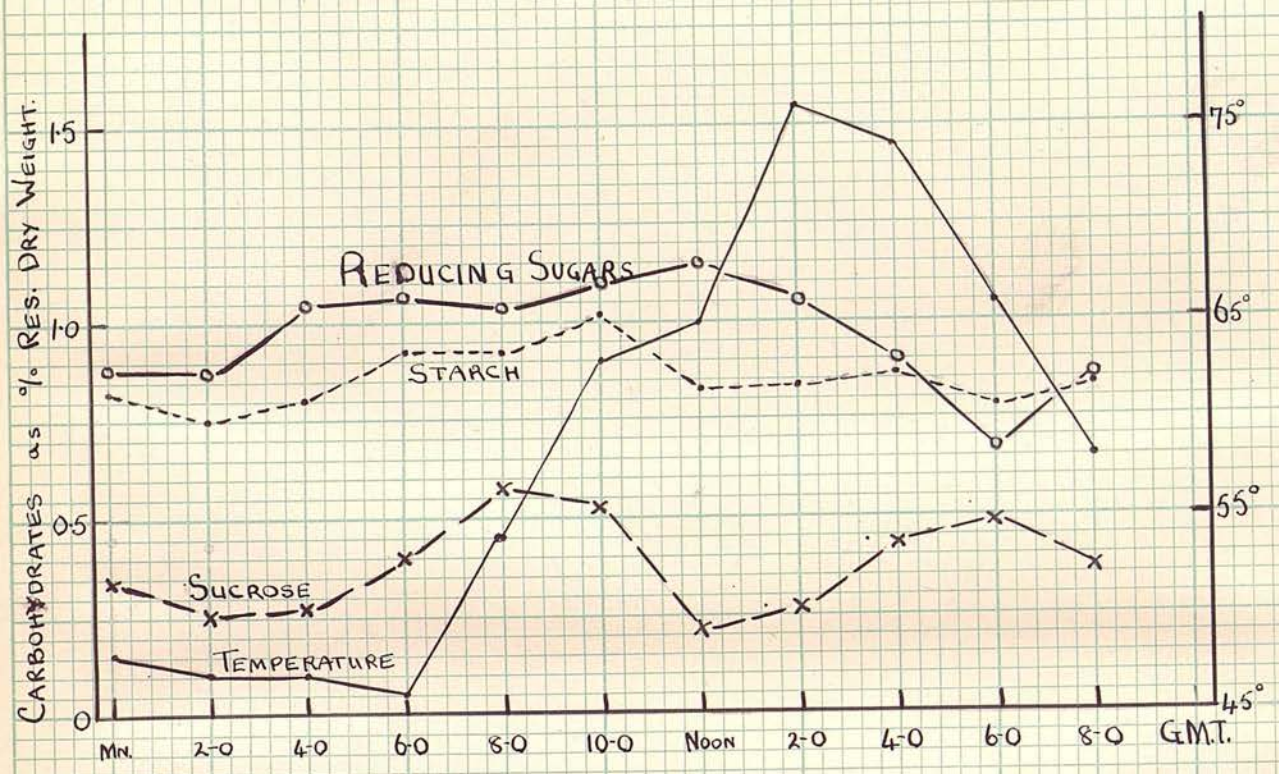

FIGURE 1. DIURNAL VARIATIONS IN CARBOHYDRATES OF THE LAMINA OF PRESIDENT SERIES 1. AGE 20 DAYS.

EXPERIMENTAL OBSERVATIONS.

Diurnal Variations in the Carbohydrates of the Leaf

President, Series I. Age, 20 days.

The diurnal variations in reducing sugars, sucrose and starch in the leaves of 20 day old President are given in Figure 1. The first point of interest to be noted from these curves is that all three forms of carbohydrate rose during the early part of the day. The rise in reducing sugars was most marked at the commencement of the period of increase, shortly after dawn, whilst sucrose rose very slowly at first and then more rapidly as the day progressed. Sucrose reached a maximum value between 8.0 a.m. and 10.0 a.m. followed closely by starch whilst the maximum value for reducing sugars occurred at noon coincidentally with secondary minima in starch and sucrose*. After noon reducing sugars/

* N.B. These secondary minima in starch and sucrose are at present inexplicable. They occur in every diurnal investigation, however, and as attempts to relate them to failures in general light intensity have not been substantiated it is possible that the cause is related to the situation and/or construction of the greenhouse in which the plants were grown.

sugars progressively decreased whilst sucrose and starch again rose, the latter to a very small extent only.

It may be argued from the accumulation of carbohydrate between 4.0 a.m. and noon, that is during the period of increasing light intensity, that formation of sugars by photosynthetic activity took place and that the rate of formation was greater than the rate of utilisation. From the order in which the curves begin their upward trend it would seem that reducing sugars accumulated first and that condensation of these sugars to starch and sucrose was subsequently a concomitant of this accumulation. After noon, and therefore with decreasing light intensity, the rate of formation of sugars would appear to have decreased and to have been reflected primarily in diminished values of reducing sugars. When the concentration of reducing sugars reached a minimum value, at 6.0 p.m., there is indication that reinforcement by hydrolysis of the temporary storage products, namely sucrose and starch, took place and that subsequently these latter formed a source of supply of carbohydrate for use within the leaf.

TABLE/

TABLE 1

MEAN VALUES	LAMINA		PETIOLE
	Gms. % R.D.W.	% Tot. Carb.	Gms. % R.D.W.
Red. Sugs.	0.973 ± 0.040	44.20 ± 1.46	0.274 ± 0.076
Sucrose	0.376 ± 0.035	16.95 ± 1.36	1.183 ± 0.050
Starch	0.854 ± 0.022	38.91 ± 0.36	0.368 ± 0.060

The mean values about which the fluctuations in carbohydrates occurred are given in TABLE 1. These data are of considerable interest in that they show reducing sugars to have been the predominating form of carbohydrate in the leaf blade whilst sucrose, which was at very low values in the leaf, predominated in the petiole. In this respect the results are quite the contrary of those recorded for the potato by DAVIS and SAWYER (1916), CLEMENTS (1930) and BARTON WRIGHT and McBAIN (1932). The high sucrose/hexose ratios in the leaves and the low ratios in the petioles reported by these workers have been corroborated by the results of the later observations upon the present material and an explanation of the inverse ratios found in President Series 1 must be sought in a consideration of the leaf as a growing organ since it has been already stated/

stated that the material under discussion was composed of young expanding leaves.

In this connection the observations of STONE (1933) are of interest. This author has presented detailed evidence to show that the growth of potato leaves, as measured by increase in area, follows an S-shaped curve with the maximum rate of increase extending over a period of 10-15 days from the time that the leaf is 1 cm. in length. Stone has suggested further that growth during this period is due more particularly to cell differentiation than to cell division in meristematic tissue. Further evidence of growth, in a wider application of the term, may be found in the observations of BUNZEL (1914). Bunzel has measured the seasonal increase in weight of single potato shoots and his data may be interpreted to show that although the maximum weight was not attained until about the 67th day of growth, the greatest rate of increase occurred before the plants were 40 days old.

Clearly, then, the present material was sampled during a very active period of growth when the leaves, since none was more than 20 days old, were passing through stages of rapid extension and increase in weight. It is not unreasonable to assume, therefore, that metabolism would be conditioned to the support of these growth activities and also, in the/

the light of the observations of PRIESTLEY (1929), that the utilisation of carbohydrate in tissue synthesis, for example the synthesis of cellulose and other stable products of cell walls and permanent tissues, would be predominantly a feature of metabolism at this stage in the seasonal history of the leaf.

WENT (1898), in a comprehensive study of the carbohydrates of the sugar cane, found that reducing sugars were always present in the largest quantities in those regions where rapid growth was taking place. He suggested that these sugars have a definite function in the support of growth both as the substrates for the synthesis of complex carbohydrates, a suggestion which ONSLOW (1931) has accepted and extended in the light of biochemical evidence, and also as the most suitable sugars for the establishment of the high internal pressures necessary in cell extension.

The present evidence with regard to the relative amounts of reducing sugars and sucrose in the growing leaves of the potato give corroboration to Went's findings and it is possible to suggest that in these leaves the balance of metabolism is controlled by the requirements of the leaf as a growing organ and that the photosynthetic activities of/

of the leaf are conditioned to supply the materials necessary to meet these requirements. As a growing organ the trend of metabolism is in the direction of carbohydrate utilisation and, in consequence, the levels of sucrose and starch, which serve as temporary storage products, are low in relation to that of reducing sugars upon which considerable demands are made in support of respiratory and synthetic activities. On the other hand, when conditions are favourable for the maintenance of carbon assimilation, that is during the daylight portion of the diurnal period, photosynthetic activity is sufficiently strong to throw the balance temporarily in favour of carbohydrate formation and the accumulation of reserve products in the manner previously discussed.

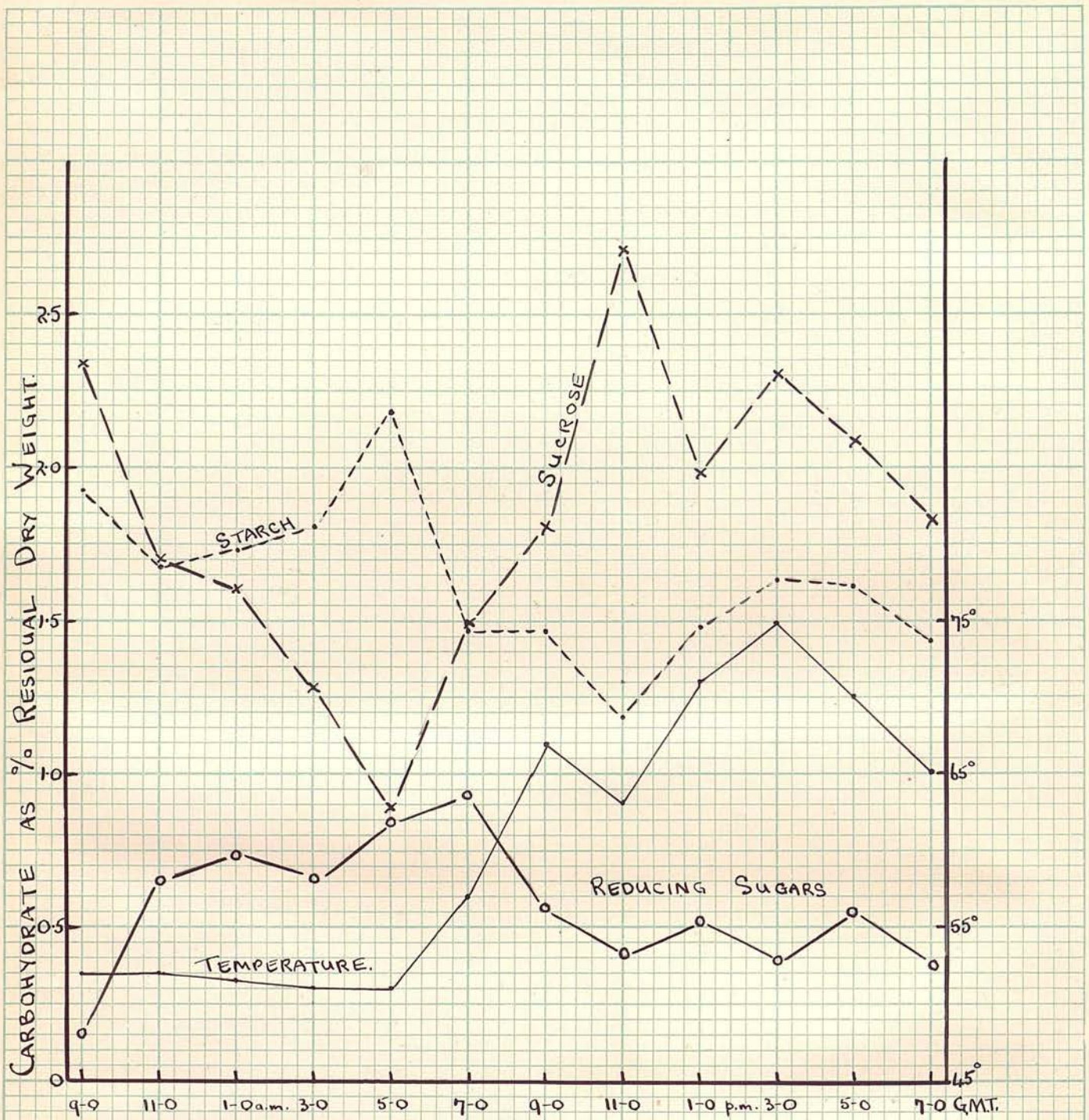

FIGURE 2. DIURNAL VARIATIONS IN THE CARBOHYDRATES OF THE LAMINA OF PRESIDENT SERIES 2. AGE 44 DAYS.

President Series 2. Age, 44 days.

A striking difference between the metabolism of leaves at 44 days old and that of young leaves is at once apparent in a comparison of the data given for President Series 1 with those for President Series 2 presented in Figure 2 and Table 2. In the latter series sucrose and starch had increased appreciably over their former values and reducing sugars had decreased slightly. The extent of fluctuation of sucrose and starch had also increased and sucrose was quite evidently the predominant sugar.

TABLE 2

MEAN VALUES	LAMINA		PETIOLE
	Gms. % R.D.W.	% Tot. Carb.	Gms. % R.D.W.
Red. Sugs.	0.564 ± 0.061	14.42 ± 1.64	0.888
Sucrose	1.780 ± 0.152	44.21 ± 3.15	0.936
Starch	1.636 ± 0.072	41.36 ± 2.02	1.655

The fact that sucrose was most abundant and fluctuated in almost linear fashion with time draws attention to the work of DAVIS and SAWYER (1916) who have stressed similar features in their potato material in order to support the contention of/

of DAVIS, DAISH and SAWYER (1916) that sucrose is the primary sugar formed directly in photosynthesis. The chief grounds upon which these authors based their claim were that sucrose preponderated in the leaf during the day; that fluctuations in sucrose were greater than those in hexoses and linear in fashion; and that "unless saccharose is a primary product it is difficult to see why it should predominate in the leaves of such different types as the potato, the vine etc. in none of which is cane sugar the storage form." The absence of mannose from leaves was taken to indicate that the enol conversion of glucose to fructose, considered to be a necessary step in the condensation of hexoses to sucrose, did not take place and that hexoses could not be the primary sugars of photosynthesis on this account. These various arguments have since been subject to general criticism on a multitude of grounds. Thus PRIESTLEY (1924) has pointed out that the intermediate stages in synthetic processes are passed through rapidly and that in consequence the first sugar formed in photosynthesis would neither accumulate to any marked extent nor show fluctuation in amount. CLEMENTS (1930) and BARTON WRIGHT and PRATT (1930) have reasoned that since the conversion of glucose to fructose/

fructose through the enolic form requires an alkaline medium, the acid medium of the leaf is entirely unsuitable for this reaction. CLEMENTS, loc. cit., has added further criticism in the light of his own data drawn from potato, soy bean and sunflower. The results he obtained from four investigations of the diurnal carbohydrate variations in the potato, which are corroborated by the results obtained from the two other species, show that sucrose, particularly towards the end of the season, is not always the form of sugar most abundant in the leaves and that starch and hemicelluloses may also, under certain conditions, fluctuate to a much larger extent than simple sugars. This author has concluded that simple sugars, probably both pentoses and hexoses, may be among the first formed sugars of photosynthesis. In forming this opinion Clements drew attention to the fact that in his material the fraction of carbohydrates estimated as simple sugars almost always increased prior to sucrose which he considered to be a temporary storage product.

It has already been seen that in the early stages of growth in the potato low values for sucrose were obtained and that sucrose increased in diurnal time after increase in reducing sugars. The present data, which, it must be emphasised, are quite/

quite corroborative of Davis and Sawyer's experimental results for the leaves of potato plants in the pre-flowering condition, show a similar lag of sucrose formation behind increase in reducing sugars immediately after dawn. This fact may be used as evidence in support of the view that reducing sugars, and not sucrose, are the first recognisable sugars formed as a result of photosynthetic activity. The subsequent fluctuations in reducing sugars, sucrose and starch may be interpreted as indicative of a high rate of sugar formation resulting in the accumulation of the temporary storage products of which sucrose is most readily produced when the rate of formation is high and increasing and starch when the rate of formation, although great, is diminishing. The progressively decreasing amounts of sucrose and starch during the night, accompanied by increase in reducing sugars, points to hydrolysis of starch to hexoses and the removal of soluble sugars from the leaf. The data are insufficient, however, to indicate whether this removal of soluble sugars is by utilisation in respiration and synthesis or by transport.

Clearly, then, the balance of metabolism at this stage of growth is strongly in favour of carbohydrate/

carbohydrate formation in excess of utilisation, as may be judged from the large diurnal fluctuations in sucrose, and the general trend of seasonal metabolism is towards carbohydrate accumulation as is evident from the greatly enhanced mean values of sucrose and starch in comparison with those of the earlier sampling.

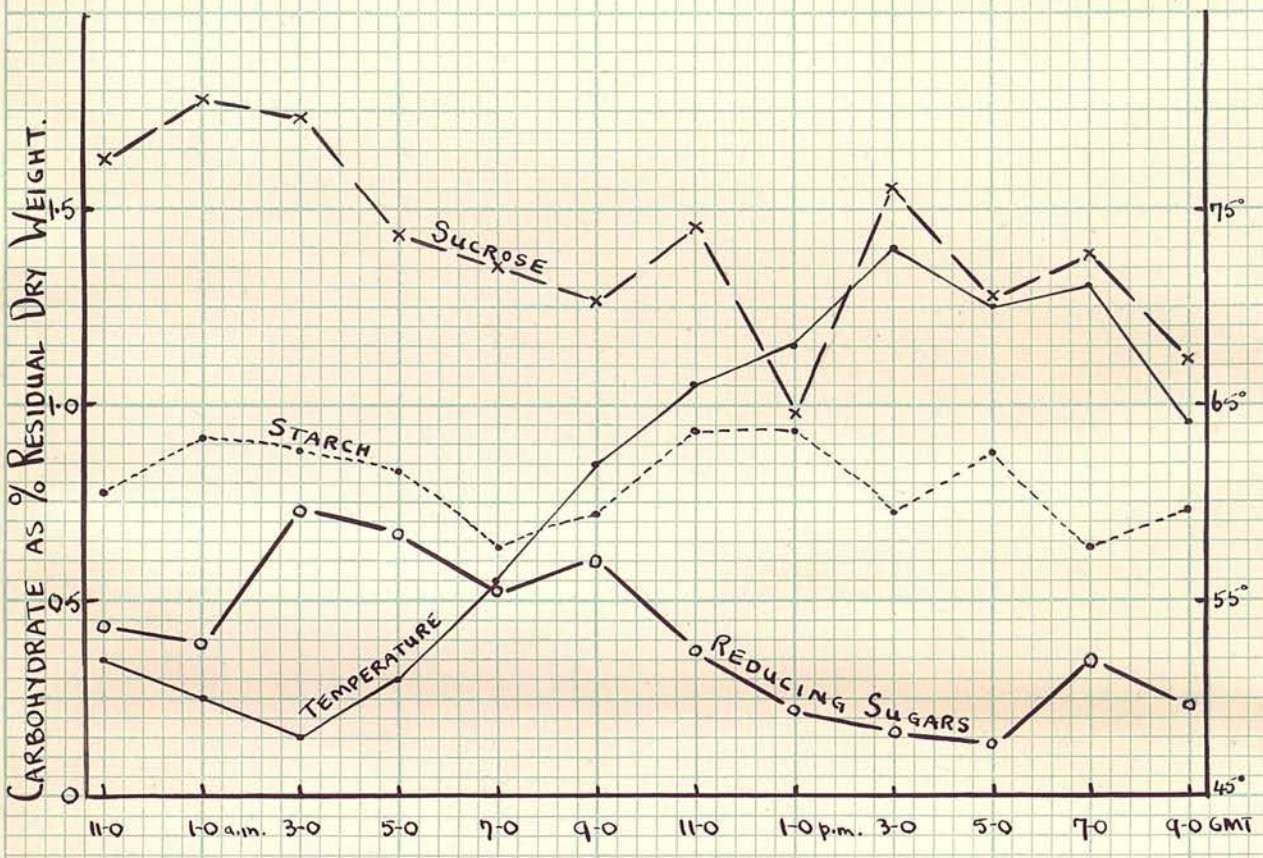

FIGURE 3. DIURNAL VARIATIONS IN CARBOHYDRATES OF THE LAMINA OF ARRAN VICTORY SERIES 1. AGE 30 DAYS.

Arran Victory. Series 1 Age, 30 days; and
Arran Victory. Series 2 Age, 72 days.

The main features of the curves showing diurnal fluctuations in the carbohydrates of the laminae of both series of Arran Victory, Figures 3 and 4, are in essence the same as those for President Series 2. The relations between the three carbohydrates indicate the formation of sucrose and starch during the day and the hydrolysis of starch to reducing sugars and the removal of soluble forms from the leaf at night. Differences in the levels about which the diurnal fluctuations took place and also differences in the shapes of the curves for reducing sugars may be attributed to seasonal effects and will be discussed in this connection. It is of interest to note, however, that both the diurnal fluctuations and the levels of the three carbohydrates of Arran Victory Series 1 approach very closely those of President Series 2, whereas the fluctuations in Arran Victory Series 3, although very similar in their relation with time to those of President Series 2, took place about mean levels suggestive of comparison with President Series 3. It would seem, therefore, that the second series of Arran Victory is representative of a transitional stage/

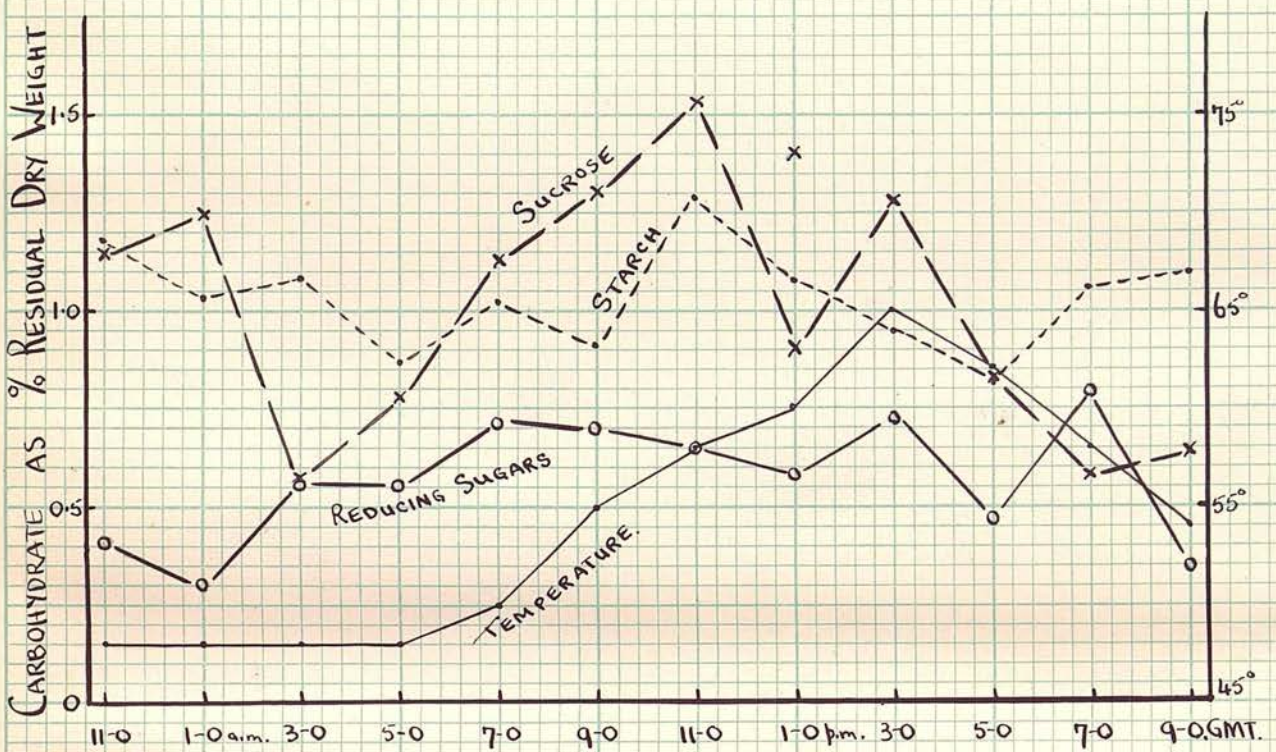

FIGURE 4. DIURNAL VARIATIONS IN CARBOHYDRATES OF THE LAMINA OF ARRAN VICTORY SERIES 2. AGE 72 DAYS.

stage of metabolism between that of carbohydrate accumulation suggested for President Series 2 and that of carbohydrate depletion which, as will be shown, accompanies the onset of senescence.

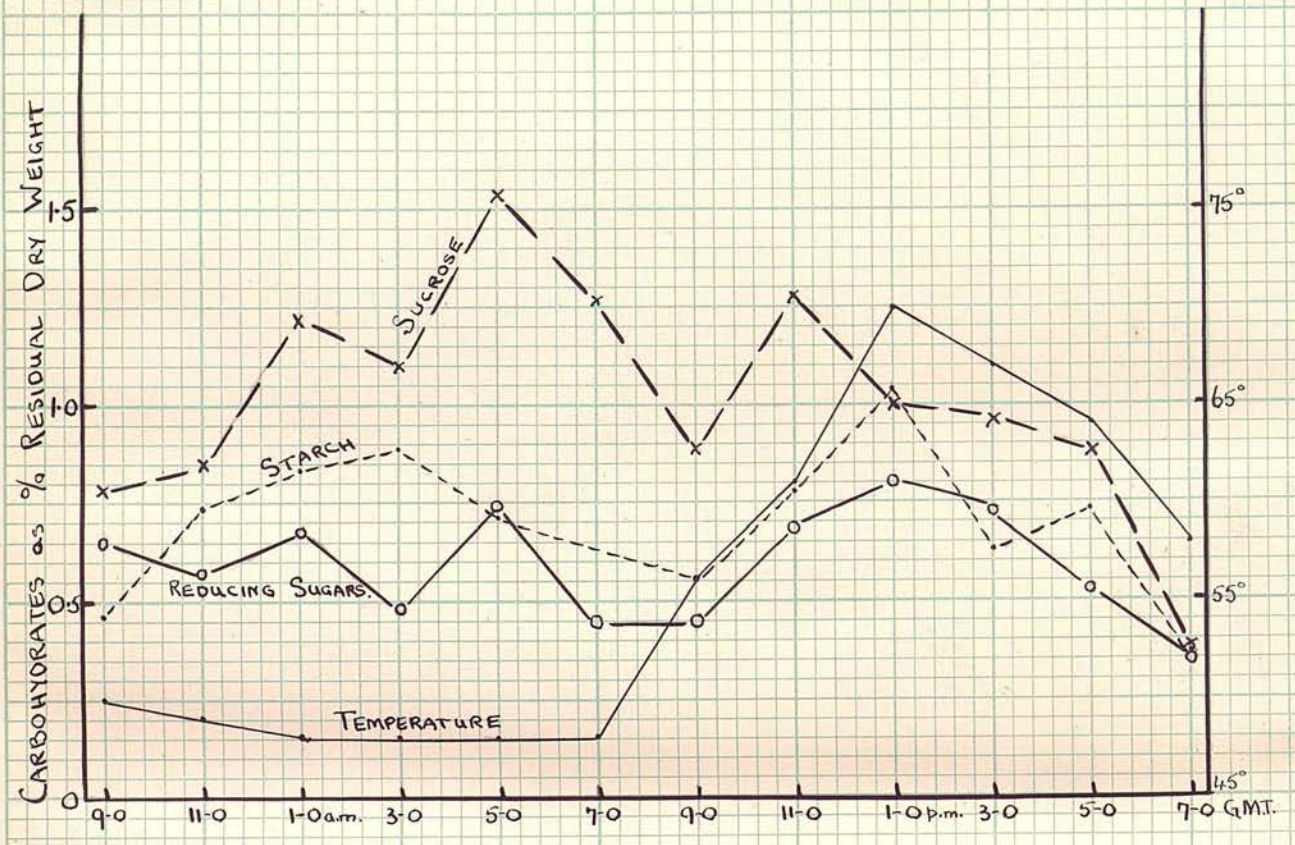

FIGURE 5. DIURNAL VARIATIONS IN CARBOHYDRATES OF THE LAMINA OF PRESIDENT SERIES 3. AGE 86 DAYS.

President Series 3. Age, 86 days.

The carbohydrate curves for President Series 3, present a totally different appearance from those provided by the material sampled earlier in the season. It will be seen by inspection of Figure 5 that between the hours of 9.0 a.m. and 1.0 p.m. the curves follow the normal daytime trend suggestive of photosynthetic activity resulting in carbohydrate formation in excess of utilisation and transport. The downward trend of all three curves between 1.0 p.m. and 7.0 p.m. is also quite normal and readily interpreted as showing a reduction of synthetic activity with decreasing light intensity and a consequential removal of the temporary storage products. During the night, however, that is between 9.0 p.m. and 5.0 a.m., there was a marked increase in all forms of carbohydrate but chiefly in sucrose and starch. CLEMENTS (1930) has also observed a nocturnal increase in carbohydrate in the older leaves of his potato material and has suggested that the increase was due to transference and condensation of sugars from the petiole. The data submitted by BARTON WRIGHT and McBAIN (1933) for the leaves of potatoes which they describe as approaching senescence show a similar increase in each carbohydrate at night and further observations

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by DAVIS, DAISH and SAWYER (1916) show that in the mangold leaf sampled in September and again in October, hexose and sucrose fluctuations and the levels of the two sugars were greater during the night than during the day. It would appear, therefore, that the phenomenon is intimately associated with the onset of maturity and/or the transfer of carbohydrate reserves to the winter storage organs. BARTON WRIGHT and McBAIN loc. cit. have discussed the carbohydrate metabolism of leaves in the conditions approaching senescence and have suggested that "at this stage in the life of the healthy plant photosynthesis has either entirely ceased or its products are very small in amount, and the formation of soluble sugars is brought about by the hydrolysis of reserve starch that has been previously built up in the leaf blade and not by photosynthesis." This suggestion arose out of a consideration of a series of regression equations involving four variables namely, hexoses, sucrose, starch and temperature. The statement quoted may interpret correctly these equations but it is difficult to understand it in the light of the facts supplied by their data. According to the hypothesis advanced, increase in soluble sugars should be accompanied by a corresponding decrease in starch. The curves given on

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page 538 of their publication show, however, that not only did hexoses, sucrose and starch in their material increase together between 2.0 a.m. and 4.0 a.m. but also that hexoses and sucrose fluctuated considerably both in time and in amount throughout the day whilst starch remained almost constant in level and at very low values. In the light of the present data and also of the facts supplied by Barton Wright and McBain, it would appear much more probable that the onset of senescence is accompanied by the hydrolysis of reserve products other than starch e.g. hemicelluloses (CLEMENTS 1930), glucosides and pentosans (DAVIS and SAWYER 1916).

BLACKMAN (1919) has stated that there is evidence that annual plants at the end of their period of growth may decrease considerably in dry weight and MILLER (1931) has brought together evidence of a similar nature. Although such a decrease cannot be substantiated in fact by the present data the course of events shown in Figure 5 would appear to indicate that during this period of near maturity in the potato the carbohydrate reserves of the leaves, including sucrose and starch, are hydrolysed and removed to the storage organs. The curves indicate, indeed, that hydrolysis of the more permanent reserves may take place to such an extent/

extent during the night that recondensation of the simple sugars formed in hydrolysis to temporary storage products, in which form they may be held readily available for transport, is necessitated.

There are difficulties which arise in accepting this explanation of the nocturnal increase in carbohydrates, particularly with regard to the enhanced values of sucrose. The formation of sucrose is dependent upon a supply of glucose and *y-fructose and whilst there is strong direct evidence that glucose is the main product in the hydrolysis of polysaccharides and carbohydrate derivatives in general there is little proof that y-fructose may also arise in this way. ONSLOW (1931), however, has assembled evidence derived from sugar feeding experiments on the one hand and desiccation experiments on the other to show that starch and sucrose are interconvertible. The mechanism suggested is based upon the assumption that active unstable y-hexoses are formed in hydrolysis and that in this active condition y-glucose and y-fructose are interconvertible. If this hypothesis be accepted and applied to the circumstances obtaining in the material under discussion, then it would seem that the/

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*y- = gamma.

the products of hydrolysis of reserve substances in the leaf are determined by two factors, firstly, the equilibria of the soluble sugars and secondly, the rate of transport of these latter from the leaf. In other words, the conditions which determine the forms in which carbohydrate accumulates during the night when the primary forms of sugar are derived by hydrolysis are similar to those obtaining during the day when the primary sugars arise de novo.

It has already been indicated that during the daylight period the normal synthesis of carbohydrate takes place and it is suggested, therefore, that the hydrolysis of reserve products is controlled by the level of soluble carbohydrates, particularly of the unstable forms, within the leaf. Thus when photosynthetic activity is resumed in the early morning with the consequent production of reducing sugars, the conditions become unfavourable for hydrolysis which, in consequence, ceases. At night, on the other hand, photosynthesis is no longer active and the conditions favour hydrolysis.

From the above discussion of the carbohydrate relations within the potato leaf at this stage in its seasonal history it would appear that metabolic activities are directed chiefly towards the/

the supply of soluble sugars for transport and storage in the appropriate organs, namely, the tubers. A comparison, to be made later, of the petiolar data for each of the diurnal periods will offer corroboration of this view.

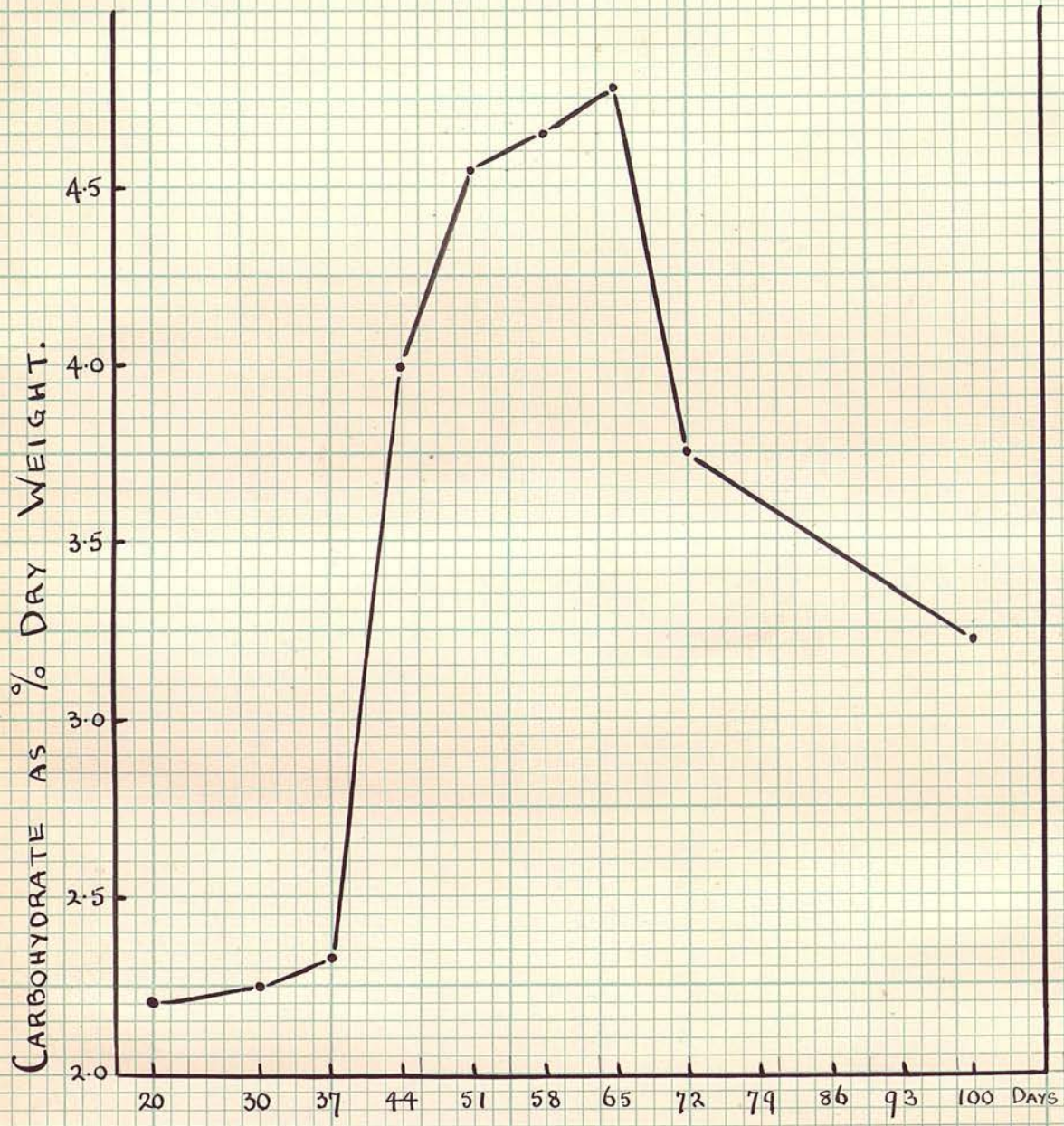


FIGURE 6. SEASONAL VARIATIONS IN TOTAL CARBOHYDRATE OF THE LAMINA OF PRESIDENT.

Seasonal variations in total carbohydrates.

President.

The curve showing the seasonal variations in the total weak-acid-hydrolysable carbohydrates of President leaves is given in Figure 6. This curve can be resolved into three distinct portions covering the periods 20-37 days, 44-72 days and 72-100 days, respectively. The first of these periods may be considered, in the light of STONE'S (1933) evidence, as representative of the carbohydrate content of leaves in their actively growing stages. Over the whole of this period, although the curve shows a slight tendency to rise, the carbohydrate content was low and this fact would appear to offer corroboration of the trend of metabolism adduced for President Series 1, namely, that the utilisation of carbohydrate formed in photosynthesis is complete in growing leaves.

The second portion of the curve is quite characteristic of carbohydrate accumulation and thus fully substantiates the interpretation that has been made of the diurnal trend of metabolism in President Series 2 which was sampled at the commencement of this period.

The gradually diminishing values of carbohydrate/

carbohydrate which occur in progressive fashion from 72 days onwards are of particular interest since they serve as a measure of support for the suggestion made in connection with President Series 3 that the onset of maturity is accompanied by a decrease in the reserve products accumulated in the leaves during the grand period of carbohydrate formation.

Although the carbohydrate fractions at each of the weekly intervals were not estimated, an indication of the seasonal changes in the individual carbohydrates is given in the mean values calculated from each of the diurnal series investigated. These values are tabulated in Table 3.

TABLE 3

MEAN VALUES	Gms. per 100 Gms. R.D.W.			% Total Carbohydrate		
	20 days	44 days	86 days	20 days	44 days	86 days
Starch	0.854	1.636	0.801	38.91	41.36	32.54
Red. Sugs	0.973	0.564	0.594	44.20	14.42	25.55
Sucrose	0.376	1.780	1.011	16.95	44.21	41.82
Tot. Sugs	1.349	2.344	1.695	-	-	-

It will be seen from this table that starch and sucrose were at their greatest values in President Series

2/

2 whilst reducing sugars were at their lowest values at this time. The decrease in total carbohydrates towards the end of the season was accompanied by a decrease in starch and sucrose and the values calculated as percentages of the total estimated carbohydrates show that the decrease was relatively greater in starch than in sucrose. Reducing sugars, on the other hand, although they decreased slightly between 20 and 44 days and increased slightly between 44 and 86 days, showed little variation in relation to the dry weight. Their relationship with regard to total carbohydrates was considerably affected by the variations in sucrose and starch, however, as will be seen from the mean values calculated on the proportional basis.

When considered in relation to the seasonal curve these data serve to emphasise the point previously discussed in connection with diurnal metabolism, that accumulation of carbohydrate during the pre-flowering stages of growth is partly, at least, due to accumulation in sucrose and starch. In addition they may be extended to show that when depletion of carbohydrate is initiated towards the end of the growing season, starch and sucrose are affected, the former to a greater extent than the latter, and that the relative accumulation of reducing sugars is a definite trend of metabolism in the leaf at this time.

FIGURE 7. SEASONAL VARIATIONS IN TOTAL CARBOHYDRATES OF THE LAMINA OF ARRAN VICTORY.

Arran Victory

A few words of explanation are necessary before proceeding to a consideration of the data given in Figure 7. The Arran Victory plants used as the experimental material for this investigation were originally planted in 6" pots owing to a shortage of the normal 9" type. The plants grew so strongly, however, during the early part of the season that they became pot-bound and showed a tendency towards premature ripening. In order to check this tendency, treatment was given immediately after the seasonal samples were obtained on the 58th day. Each plant was repotted and supplied with a single teaspoonful of a mixed fertiliser containing superphosphate, sulphate of potash, sulphate of ammonia and ground bone meal in the proportions of 4 : 2 : 2 : 1. In response to this treatment a new period of growth was initiated and it is interesting to note that the effect of ripening and of treatment is reflected in the curve for total carbohydrates.

TABLE/

TABLE 4

MEAN VALUES	Gms. per 100 Gms. R.D.W.			% Total Carbohydrate		
	20 days	30 days	72 days	20 days	30 days	86 days
Starch	0.463	0.803	1.035	24.47	31.02	40.35
Red. Sugs.	0.720	0.407	0.591	36.55	15.06	22.04
Sucrose	0.768	1.416	1.028	38.98	53.92	37.64
Tot. Sugs.	1.488	1.823	1.619	-	-	-

The first four observations on the curve were obtained from samples taken before the ripening effect was visible. The curve connecting these points shows a rapid increase in carbohydrate culminating in a maximum at 51 days. Two sets of data for the values of individual carbohydrates are available for this period (TABLE 4). The first set, for 20 day old plants, show that reducing sugars amounted to 0.720% of the dry weight and 36.55% of the total estimated carbohydrates, sucrose to 0.768% and 38.98% respectively, and starch was least with values of 0.463% and 24.47%. Ten days later the diurnal values for Arran Victory Series 1 were obtained. In the interval reducing sugars had dropped to 0.407% and 15.06%; sucrose had risen to 1.416% and/

and 53.92%; and starch to 0.803% and 31.02%. It is quite evident from these changes that the formation of carbohydrate in photosynthesis was overtaking its utilisation in support of growth and that the seasonal trend of metabolism was similar to that of President.

The premature ripening effect previously referred to was apparently responsible for the rapid decrease in carbohydrate values between 51 and 58 days. On the latter date the treatment was given and, presumably in response to the more favourable conditions, the decrease in carbohydrates was checked at 65 days. The second series of diurnal samples were obtained at 72 days, shortly after the balance of metabolism had swung again in the direction of carbohydrate increase. The summarised mean values for this material show that starch and sucrose were the predominating forms of estimated carbohydrates at this time whilst reducing sugars, although of low values, were slightly greater in amount than those recorded for Arran Victory Series 1. The significance of this increase cannot be estimated directly from the data available but as the diurnal curves show fluctuations in reducing sugars to be somewhat similar to those for President Series 3 it would appear that the increase can be ascribed to a seasonal effect rather than to a response to treatment.

Petioles

The estimates of carbohydrate variations in the petioles of both President and Arran Victory have been restricted to group analyses of starch, sucrose and reducing sugars for each of the diurnal periods investigated. The mean diurnal values, together with the various ratios between the soluble sugars of the lamina and those of the petiole, are given in TABLE 5, and arranged in progressive series with age of the plants irrespective of variety.

TABLE 5

PETIOLE SEASONAL VARIATIONS and RATIOS between LAMINAR and PETIOLAR SUGARS

	Series and Age	Pres. 1 20 days	A.Vic. 1 30 days	Pres. 2 44 days	A.Vic.2 72 days	Pres.3 86 days
% R.D.W.	Starch	0.368	1.581	1.655	1.702	1.086
	Red. Sugs.	0.274	0.694	0.888	0.970	2.689
	Sucrose	1.183	0.687	0.936	1.054	1.060
	Tot. Sugs.	1.457	1.381	1.824	2.024	3.749
Ratios	RS_L/S_L	2.588	0.287	0.317	0.575	0.588
	RS_P/S_P	0.232	1.010	0.949	0.921	2.537
	TS_P/TS_L	1.080	0.758	0.778	1.250	2.206
	RS_P/TS_L	0.203	0.381	0.379	0.599	1.587
	RS_P/RS_L	0.282	1.705	1.572	1.641	4.527
	RS_P/S_L	0.729	0.490	0.499	0.944	2.661
	S_P/TS_L	0.876	0.377	0.399	0.651	0.625
	S_P/RS_L	1.215	1.688	1.659	1.783	1.785
	S_P/S_L	3.147	0.485	0.514	1.025	1.048

RS = Reducing Sugars
S = Sucrose
TS = Total Sugars

Subscript L = Lamina
Subscript P = Petiole

It will be seen from this table that soluble sugars in the petioles increased progressively throughout the season and reached very high values in the 86 days old material. Over the whole period, however, sucrose values remained almost constant and the variations in soluble sugars were due entirely to increases in reducing sugars. These facts are in complete accord with those of other investigators, in so far as their data are available, and the most probable interpretation to be placed upon them is that they are indicative of progressive increase in the amount of carbohydrate transported from the leaf. The increase is particularly marked in the 86 day old plants and is corroborative, therefore, of the suggested trend of metabolism for these plants, namely, that depletion of carbohydrate in the leaf is directed towards transport of reserve materials from the leaf to the tubers.

The nature of the sugars concerned in the translocation in the potato has given rise to a good deal of speculation. DAVIS and SAWYER (1916) and CLEMENTS (1930) have expressed the opinion that since reducing sugars preponderate in the petioles they must be the chief sugars of transport. On the other hand, BARTON WRIGHT and McBAIN (1932) have presented strong evidence that sucrose is/

is the translocatory sugar. This evidence is based upon the observations

(1) that diurnal variations in the sucrose content of the petioles of their material were reflections of the variations in this sugar in the laminae;

(2) that there was a positive gradient of sucrose between the midribs of the leaves and the lower stem of the healthy plant;

and (3) that in plants affected with leaf roll, in which the phloem is often necrotic, no sucrose was found in the petioles or stem.

In the leaf roll plants there was, however, a positive gradient of hexoses between the midribs of the leaves and the lower stem. These data are highly conclusive in establishing an obligate connection between sucrose and the phloem in the conducting organs and also in showing sucrose to be a form of sugar in which carbohydrate is translocated in the healthy potato plant. They do not, however, preclude the possibility that reducing sugars are also concerned in transport. On the contrary the results from the leaf roll material would appear strongly to favour reducing sugars as normal sugars of transport.

The data provided by the present investigation although inconclusive with regard to the function of sucrose in the petiole, appear to offer fairly/

fairly conclusive evidence that reducing sugars are the chief forms in which sugar is translocated, particularly during the later part of the season, for not only do reducing sugars in the petioles increase progressively in amount during the course of the season but also the relationships between petiolar and laminar sugars increase in similar fashion. The fact that sucrose in the petioles remains fairly constant in amount may indicate that translocation of this sugar is taking place at a maximum rate throughout the season and that it is restricted to certain channels, namely, the phloem. If this is the case, then it would seem that translocation of reducing sugars may suffer no restrictions of this nature and have alternative channels as was suggested for the leaf roll material of Barton Wright and McBain.

CONCLUSIONS

An examination of the variations in the carbohydrates of the leaves and petioles of the two potato varieties President and Arran Victory over diurnal and seasonal periods has shown quite clearly, with due regard being paid to varietal differences, that the trend of metabolism in each follows a similar path and is subject to the same seasonal modifications. Three major phases of seasonal metabolism have been traced and identified with three stages in leaf growth, namely, expanding, expanded, and maturing stages.

In the young and rapidly expanding leaves reducing sugars were found to be of relatively high values in comparison with sucrose and starch and it has been argued that although the leaves function predominantly as photosynthetic organs during the day, the balance of metabolism is controlled by their requirements in support of growth. With continued expansion it would appear that the leaves become increasingly efficient with regard to photosynthesis so that a second phase of metabolism is initiated in which the supply of carbohydrate exceeds the demands for utilisation in tissue synthesis and respiration.

In/

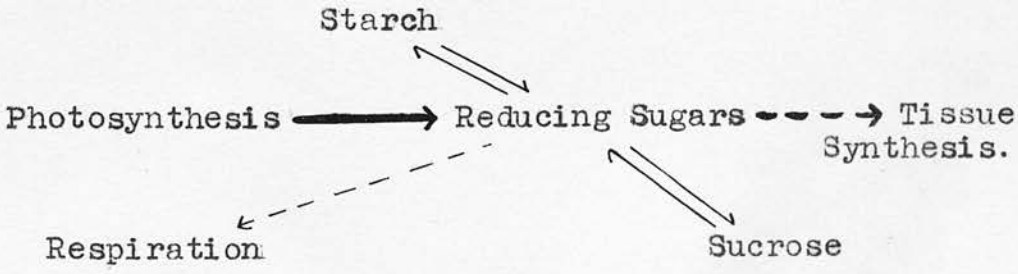
In these circumstances accumulation of reserve carbohydrate commences and the leaves would seem to serve as temporary storage organs. Sucrose and starch have been shown to be the forms in which carbohydrate may be stored temporarily and there is strong presumptive evidence to suggest that more permanent reserves are also laid down during the period of intensive photosynthesis. At the approach of maturity a third phase of metabolism has been traced in which carbohydrate removal from the leaves takes place in excess of the mean rate of formation in photosynthesis. The evidence in this direction has indicated that the temporary storage products are first reduced in amount and that these are followed by a removal of the more permanent reserves. The fact that during this period of removal petiolar sugars were of greatly enhanced values has led to the conclusion that the transfer of carbohydrate reserves from the leaves to the tubers was taking place. In addition, it has been shown that the increase in sugars in the petioles was mainly due to increased values of reducing sugars and this fact has been used, in part, to establish these sugars as the translocatory carbohydrates in the potato leaf.

Throughout these three phases of metabolism reducing sugars have been shown to vary but slightly in/

in amount over any one diurnal period and, in the light of the facts submitted, the seasonal differences which have been observed may be ascribed as due mainly to variations in the standard of expression since it has been indicated that reducing sugars were of greatest values during the early stages of growth, when dry weight through tissue synthesis was presumably increasing, and that they increased again to a very slight extent at the end of the season when dry weight was presumably decreasing by depletion of the carbohydrate reserves. The evidence which has been discussed has also led to the conclusions that a form of reducing sugar is the first recognisable sugar to accumulate as a result of photosynthetic activity; that polysaccharide degradation leads primarily to the formation of reducing sugars; and that reducing sugars are the forms in which carbohydrate, at least at the end of the season, is translocated. There is good reason for the assumption, therefore, that these sugars are the focus point of carbohydrate metabolism and that the complex reactions between the leaf carbohydrates are controlled by the concentration of reducing sugars in the leaf. If this assumption be used as a basis it is possible to indicate/

indicate the metabolic activities of the potato leaf at each of its three main stages of growth, namely, expanding, expanded, and maturing, by the following schematic diagrams. In each of these diagrams direct evidence is indicated by unbroken lines, presumptive evidence by broken lines and the main directions of the reactions by heavy lines.

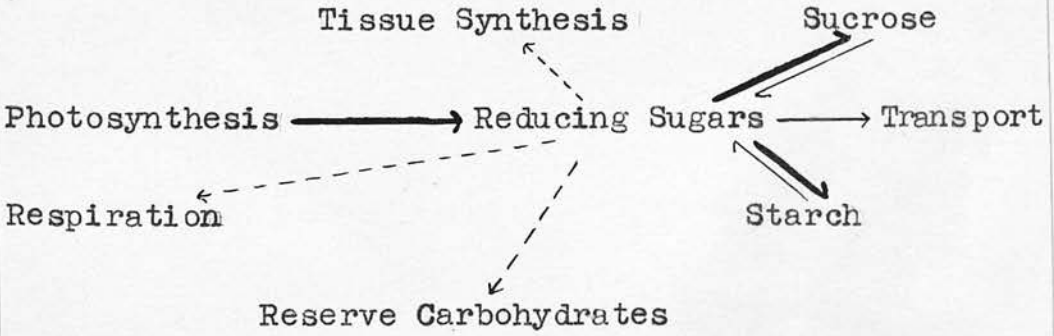
The data provided by an examination of President Series 1 have given the facts that sucrose and starch are relatively low in amount compared with reducing sugars; that all three carbohydrates increase during the day and decrease at night; and that petiolar sugars are relatively low with sucrose predominating. These facts have been interpreted to show that the main line of synthesis is in the direction photosynthesis ⟶ reducing sugars ⟶ tissue synthesis and that the sucrose and starch relationships with reducing sugars are reversible and dependent upon the concentration of reducing sugars. The general scheme of metabolism would appear to be:



The/

The transport of carbohydrate seems to be of little consequence at this stage of growth although, in the light of the evidence of STONE (1933) who has suggested that the growth of a leaf is directly affected by the initiation of growth in a leaf above, it is possible that transport into the leaf may take part at an earlier stage. In the present case, however, the leaf appeared to have reached a stage at which it was quite self-supporting.

The second phase of metabolism has been indicated in the data obtained for President Series 2 and Arran Victory Series 1. The facts here are that sucrose and starch increase rapidly and to a great extent during the day; that both decrease at night; that both are of relatively high values in comparison with reducing sugars; and that in the petioles reducing sugars have increased over their former values. The main line of synthesis would appear to be in the direction of sucrose and starch formation and, at a later stage, presumably towards reserve carbohydrate formation. The scheme of metabolism is therefore:

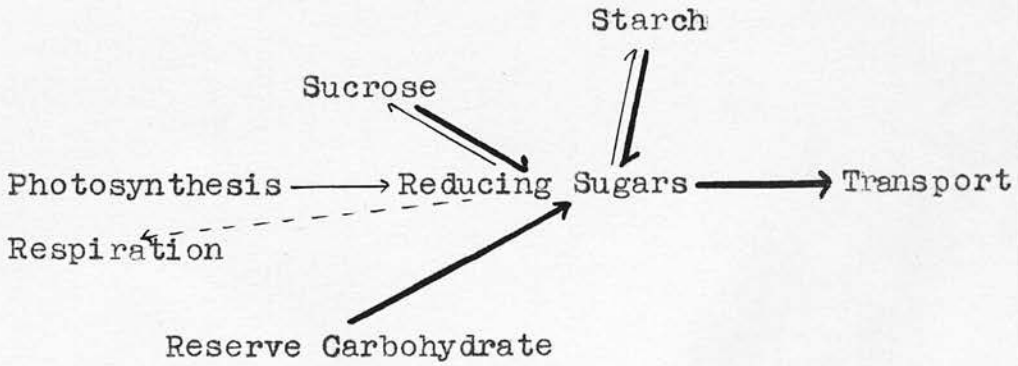


It/

It is possible that the formation of reserve carbohydrates takes the place of tissue synthesis in the progressive course of time.

The data from Arran Victory Series 2 are indicative of a midway stage between the scheme outlined above and that of the maturing leaves of President Series 3. These data were, however, complicated by treatment during the course of the season and no absolute value can be attached to them.

In President Series 3 the carbohydrate relations of the leaf were found to be indicative of two distinct trends of metabolism one of which was active during the day and the other during the night. During the day photosynthesis was active and the normal trend of sugar and starch accumulation took place. During the night a similar accumulation was evident and the data have been interpreted as indicative of hydrolysis of reserve products. The general scheme of metabolism representative of the period is therefore:



During/

During the early stages of maturity the reactions starch ⟶ reducing sugars ⟶ transport, and sucrose ⟶ reducing sugars ⟶ transport are probably the main lines of sugar depletion but later there is definite indication that the main trend is in the direction reserve carbohydrate ⟶ reducing sugars ⟶ transport. Photosynthetic products are relatively small throughout this period and are directed ultimately towards transport.

SUMMARY.

(1) The variations in reducing sugars, sucrose and starch in the normal leaves of the potato varieties Arran Victory and President have been followed over five diurnal periods.

(2) The seasonal variations in total carbohydrates have also been determined and examined in the light of the evidence derived from the diurnal investigations.

(3) The reducing sugars of the leaf have been shown to vary only slightly in amount over diurnal and seasonal periods of time and the evidence has led to the suggestion that these sugars are the first recognisable products of photosynthesis, that they are the basic sugars in metabolism and that they are also the forms in which carbohydrate is transported out of the leaf during the latter part of the season.

(4) Sucrose and starch have been shown to play the parts of temporary storage products in the carbohydrate economy of the potato leaf.

(5) Three major trends of carbohydrate metabolism, each of which may be identified with a particular stage of leaf development, have been recognised and/

and discussed.

(6) In the early vegetative stages of growth the balance of metabolism has been shown to be controlled by the requirements of the leaf as a growing organ and the photosynthetic activities to be conditioned to supply the materials necessitated by these requirements.

(7) The pre-flowering stage was found to be accompanied by a high rate of carbohydrate formation and by the accumulation of the temporary reserve carbohydrates. It has been suggested that as tissue synthesis gives place to the synthesis of the more permanent forms of carbohydrate reserves the leaf ultimately functions not only as the seat of photosynthesis but also as a temporary storage organ.

(8) During the post-flowering stages depletion of the carbohydrate reserves was indicated by decreased values of starch and sucrose and by relatively increased values of reducing sugars. Greatly increased values of reducing sugars in the petioles led to the suggestion that carbohydrate was transferred from temporary storage in the leaves to conditions of more permanent storage in the tubers. The nocturnal increases in carbohydrate during this period led to the further suggestion that the hydrolysis/

hydrolysis of semi-permanent reserves contributed to the sugars available for transport and that the mechanism of hydrolysis was controlled by the level of the active sugars in the leaf.

(9) The carbohydrate metabolism of the leaf in each of these three phases has been illustrated in schematic form.

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SECTION I

Part 2.

A Comparison of the Metabolism of Mosaic Infected Potatoes with that of Normal Potatoes.

II. Variations in the Carbohydrate and Total Nitrogen Content of Mosaic Infected Leaves as compared with Normal Leaves.

C O N T E N T S

INTRODUCTION.

One of the most commonly expressed symptoms of virus infection is that of leaf chlorosis or mottling characteristic of the large group of true mosaic diseases. Simple mottling, however, is often accompanied by leaf distortion, reduction in size of plant and plant organs, and by necrotic lesions. These gross morphological and anatomical abnormalities, which give rise to the descriptive names of crinkle, curly dwarf, ringspot, streak, etc. for many of the diseases evinced by mosaic viruses, may be quite sufficient in themselves to cause serious disturbances in metabolism and thus obscure the real effect of the virus upon the physiological balance of the host. In attempting to ascertain the primary effect of virus upon metabolism it is essential, therefore, that the material under examination should be free from gross malformations and necrotic symptoms so that secondary effects due to these symptomatic causes may be small and readily traced. The material for the present investigation was chosen with due regard to the elimination, as far as possible, of such secondary effects and relates to the potato varieties President and Arran Victory infected with the X potato virus of

SMITH/

SMITH (1931). The symptoms of infection with this virus upon the two potato varieties used are restricted to slight chlorotic mottles situated in the interveinal tissue but in close proximity to the veins. The leaf surface remains quite flat and there are no attendant puckerings or necrotic symptoms. The disease is usually referred to as mild or simple mosaic. The symptoms upon the variety Arran Victory are slightly more severe than those on President but this is due entirely to slightly larger chlorotic areas in the former and a greater contrast between these areas and the normal areas of the leaf.

REVIEW of LITERATURE.

A review of the literature relating to the effects of mosaic diseases upon the chemical physiology of the host plant reveals a consensus of opinion that carbohydrate economy is adversely affected by the presence of one or more of the mosaic viruses. Diminished values of carbohydrates in mosaic infected plants as compared with healthy controls have been recorded for tobacco by BAILEY (1924), DUNLAP (1930, 1931), CORDINGLEY, GRAINGER, PEARSALL and WRIGHT (1934); for tomato by BREWER, KENDRICK, and GARDNER (1926), DUNLAP (1930), READ (1933, 1934), and CALDWELL (1934); for sugar cane by COOK (1926); and for potato by SCHULTZ, FOLSOM, HILDERBRANDT and HAWKINS (1919), FOLSOM (1920), MALHOTRA (1931) and STONE (1936). DUNLAP (1930) has also submitted similar evidence for mosaic infected plants of pokeweed (Phytolacca decandra), cucumber and raspberry and has concluded that plants affected with true mosaic diseases are characterised by a lower carbohydrate content and a higher nitrogen content than healthy plants.

Metabolic disturbances have been traced chiefly to disturbances in the starch - sugar relationships/

relationships. WOODS (1902) observed that although starch is formed in diseased areas of the tobacco leaf it is not readily broken down for purposes of translocation. LUDTKE (1930) also recognised a tendency towards starch immobility in mosaic infected tobacco leaves but was unable to trace any destruction of, or reduced, activity in the diastase contents of these leaves. DUNLAP (1931), on the other hand, found that although mosaic leaves of tobacco contained smaller amounts of all forms of carbohydrate, soluble sugars tended to accumulate to a greater extent in these diseased leaves. He construed this as indicating that the conversion of starch to simpler compounds took place more rapidly in mosaic leaves than in those of healthy plants. CORDINGLEY et al (1934) supported DUNLAP'S findings in so far as they were able to confirm reduced amounts of all forms of carbohydrate in the diseased leaves but their further data showed a close similarity between the relative proportions of the carbohydrates within both healthy and diseased leaves. In respiration studies, these latter authors found that although carbohydrate losses were of similar degree in both series of leaves, the losses fell chiefly upon insoluble carbohydrate in the healthy leaves and upon disaccharides/

disaccharides in the mosaic leaves.

Somewhat similar results to those reported for tobacco have also been recorded from investigations concerning mosaic infected tomato plants. BREWER and his co-workers (1926) have found consistently lower values of polysaccharides in entire tomato plants affected with ordinary tomato mosaic, but their data for reducing sugars show a tendency only in this direction whilst non-reducing sugars were variable between the two series of infected and healthy plants. An accelerated rate of removal of starch from affected leaves during the dark and a failure of the yellow areas to form starch during the day was reported by BOLAS and BEWLEY (1930) to accompany the early stages of development of aucuba mosaic in the tomato. Starch remained immobile, however, near the sources of inoculation. At a later stage, a complete local absence of starch was observed in some parts of affected leaves whilst there was a marked accumulation in others. READ (1933) has shown that shortly after inoculation with the virus of aucuba mosaic the amount of reducing sugars in affected tomato leaves increased over that of the controls. The diseased leaves were found to contain

more/

more starch than the healthy leaves during dull weather but the reverse was the case during bright periods. In a further study READ (1934) sampled healthy and diseased plants at intervals of two hours over a period of twenty hours. The results of this investigation were interpreted to show a time lag in the conversion of reducing sugars to non-reducing sugars in the diseased leaves. The mean values of reducing sugars were approximately ~~of~~ the same ~~values~~ in both healthy and diseased leaves, however, but non-reducing sugars were of smaller values in the latter.

The presence of mosaic in the potato has been shown by SCHULTZ et al. (1919) to be accompanied by an increase in the amount of sugars in the leaf and by a decrease in the amount of starch. Reducing sugars showed a greater increase than non-reducing sugars. MALHOTRA (1931) has analysed the whole aerial portions of young potato plants infected with the virus of tomato mosaic. His figures show that total carbohydrates, non-reducing sugars and starch were lower in the diseased plants and that reducing sugars were of similar values in both diseased plants and their controls. BARTON-WRIGHT and McBAIN (1933) have compared the diurnal trend of/

of carbohydrate metabolism of crinkle affected potato plants with that of healthy plants and have interpreted their data to show that fundamentally there was no difference between the two at an early stage of growth. When senescence set in they found a tendency towards carbohydrate accumulation in laminae and petioles of the diseased plants and they ascribed this accumulation to difficulties in translocation. STONE (1936) has also found an accumulation of sugars and starch in the tops of mosaic diseased potatoes during senescence. This author has brought forward evidence, in addition, to show that mosaic affected leaves are much less efficient than normal leaves in their capacity to assimilate and fix carbon.

Respiration studies have been few in number and of varied techniques. DUNLAP (1930) measured the respiration of a large number of species by suspending single leaves in tubes containing baryta. His results show that respiration, as measured by CO_2 production, was greater in young diseased leaves and smaller in older diseased leaves than in the controls. CALDWELL (1934) measured the amount of CO_2 produced by healthy and aucuba mosaic leaves of tomato over several continuous periods of 48 hours and found that the CO_2 output of diseased tissue/

tissue was invariably greater than that of healthy tissue irrespective of the standard to which the values were referred. He attributed the higher rate of respiration to an increased efficiency in those enzymes responsible for the preparation of the substrate for respiration proper. Unfortunately he made no analyses to determine upon which forms of carbohydrate the losses in respiration fell. CORDINGLEY et al. (loc. cit.) estimated the carbohydrates of half leaves of mosaic infected tobacco at the beginning of and again at the end of a 68-hour period of respiration in the dark. They found that the carbohydrate loss on a dry weight basis was the same in both healthy and diseased leaves but that the loss fell chiefly on the insoluble carbohydrates in the former and upon the disaccharides in the latter.

With regard to the nitrogen content, BAILEY (1924), DUNLAP (1930), READ (1933) and MALHOTRA (1931) have all reported a greater amount of nitrogen in the diseased material of the various species studied. BREWER et al. (1926) and CALDWELL (1934), on the other hand, found that the total nitrogen content of mosaic infected tomatoes was in some cases greater, and in others smaller than that of/

of healthy plants but that the amount tended to be the same in each. CORDINGLEY et al. (1934) estimated various nitrogen fractions in mosaic infected tobacco and found that on a dry weight basis, total nitrogen, protein N. and amino N were greater in these than in healthy leaves and that the fraction estimated by them as Rest N, i.e. the difference between soluble N and amino N, was equal in both series. When calculated relative to total nitrogen, however, protein N and amino N were still greater in the diseased leaves but Rest N was appreciably smaller. During degradation over a 68-hour period in the dark, they found that in the healthy leaves protein N decreased and amino N and Rest N increased. In the diseased leaves, on the other hand, there was little decrease in protein N, a large decrease in amino N and an increase in Rest N. They interpreted these results to indicate that amino-acid oxidation, in comparison with amino-acid formation, is relatively accelerated and that protein breakdown is considerably retarded in diseased leaves. SMITH and DUFFRÉNOY (1934) have suggested from cytological evidence that the synthesis of cytoplasmic complexes is retarded and an accumulation of amino-acids is induced in tobacco plants affected with mosaic of the vein-banding type caused/

caused by the Y potato virus.

These various data, drawn mainly from three solanaceous species infected with a variety of mosaic diseases, may be brought together and summarised to show that in mosaic infected plants, as compared with healthy plants, the amount of carbohydrate is generally lower and that polysaccharides, including starch, are most greatly affected; that the degradation of starch is retarded and that carbohydrate respiration is probably greater and falls chiefly on soluble sugars; that nitrogen is usually higher and that degradation of nitrogen is affected in a similar manner to degradation of carbohydrate, i.e. insoluble forms are less readily hydrolysed; and finally that the C/N ratio is <u>always</u> lower.

MATERIAL and METHODS.

The diseased material used in this investigation has already been described as of the two potato varieties President and Arran Victory affected with the disease of mild mosaic and, more particularly, as infected with the X potato virus. Treatment, with regard to growing conditions and sampling, was exactly similar to that for the healthy material described in a previous section and the analytical methods for carbohydrates were identical throughout.

The data upon total nitrogen have been furnished by analyses of the same material as that used for carbohydrate analysis. At each period of sampling a portion of the finely chopped mass of fresh material was extracted from the bulk, killed with xylol alone and dried to constant weight under the same conditions as the remainder since this method has been shown by PEARSALL and WRIGHT (1929) to be quite satisfactory for both carbohydrates and nitrogen. Total nitrogen was estimated by the method described by RANKER (1925) which includes nitrate nitrogen in the estimate. Weighed quantities of the redried and finely ground material were digested with concentrated sulphuric acid to which salicylic acid, sodium/

sodium thiosulphate and a trace of copper sulphate were added. After digestion was completed the clear acid solution was cooled and solid caustic soda added in excess. The liberated ammonia was then distilled off into N/10 sulphuric acid and nitrogen determined by back titration with N/10 sodium hydroxide. The results have been calculated as grams nitrogen per 100 grams residual dry weight.

EXPERIMENTAL OBSERVATIONS.

Before proceeding to a detailed comparison of the diurnal and seasonal variations in healthy and mosaic infected plants it is convenient to draw attention to a salient feature of the results to be presented. It will be observed from the data for each series of comparisons that the gross levels of the carbohydrates with regard to seasonal changes in level, and the gross trend of diurnal and seasonal variation are very closely similar in both healthy and diseased material. These facts of similarity may be used in dual fashion; firstly, to double the strength of the evidence upon which the direction of metabolism in the healthy plant has been established; and secondly, to establish the principle that the gross metabolism of the diseased plant is essentially the same as that of the healthy plant. An acceptance of this principle at this stage will avoid constant repetition in drawing attention to the fact that the differences to be found in detailed comparison are small in relation to the similarities in wide comparison.

President Series 1. Age, 20 days.

Although a similarity between the data for the diseased laminae and those for the healthy is

most/

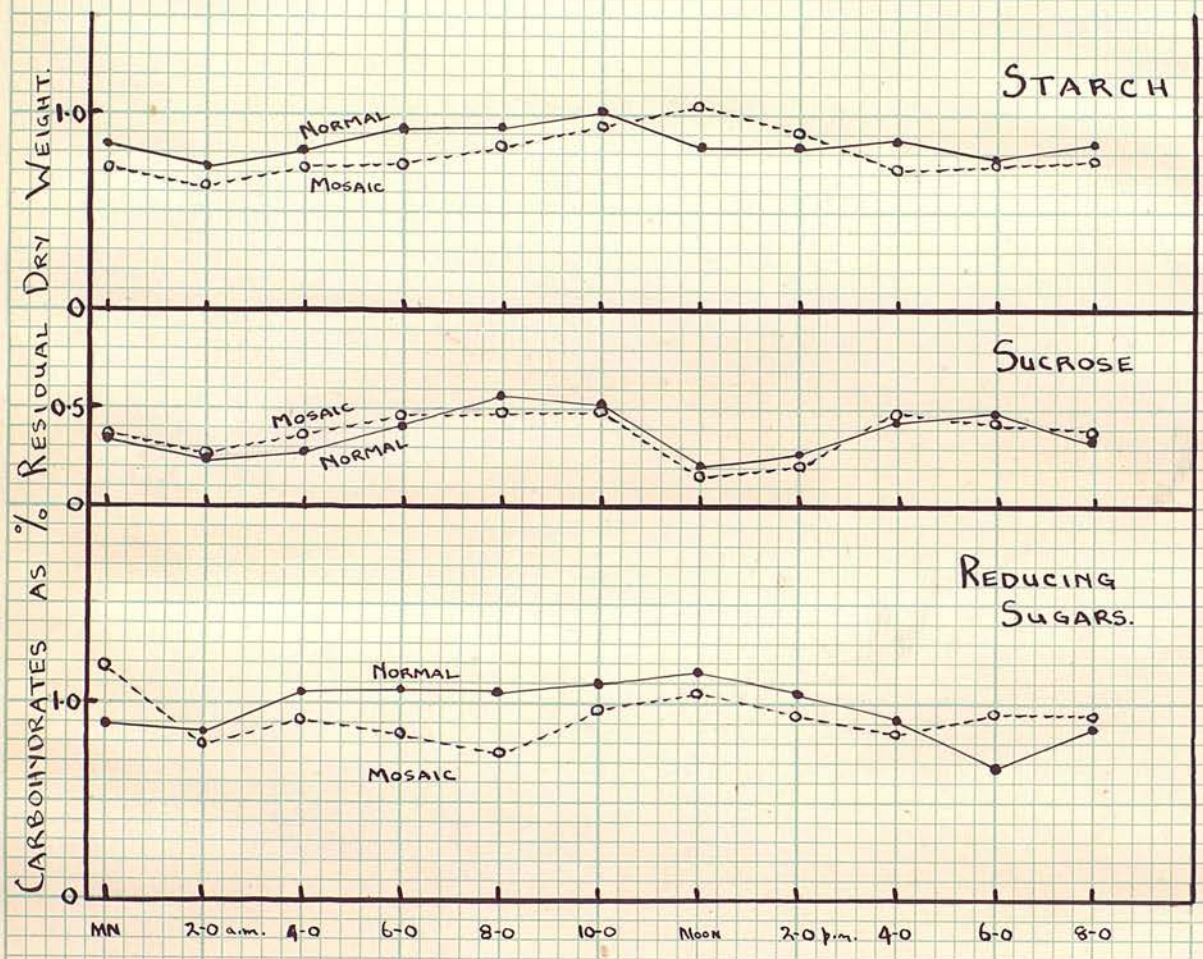

FIGURE 1. PRESIDENT SERIES 1. AGE: 20 DAYS.
DIURNAL VARIATIONS IN CARBOHYDRATES OF NORMAL AND MOSAIC AFFECTED LEAVES.

most strongly emphasised, the curves in Figure 1 and the summarised mean values in Table 1 show slight tendencies towards difference which in view of their bearing on the further results are worthy of examination. It will be seen from the curves that reducing sugars in the diseased laminae tended to fluctuate at a lower mean level during the day and at a higher mean level during the night. The diurnal mean (Table 1), however, was slightly lower than that for the healthy laminae. Sucrose values, on the other hand, were almost identical for both series of plants at all times of day and also in the diurnal means. Starch fluctuations resemble those of reducing sugars in that they took place about a lower mean value and it will be observed that they show a tendency to lag behind corresponding fluctuations in the healthy laminae.

TABLE/

TABLE 1.

MEAN VALUES		HEALTHY	MOSAIC	DIFFERENCE	D/E_d
% R.D.W.	Red. Sugs.	0.973 ± 0.040	0.939 ± 0.036	0.034 ± 0.054	0.63
	Sucrose	0.376 ± 0.035	0.382 ± 0.034	0.006 ± 0.049	0.12
	Starch	0.854 ± 0.022	0.803 ± 0.034	0.051 ± 0.041	1.24
% Total	Red. Sugs	44.20 ± 1.46	44.24 ± 1.23	0.04 ± 1.91	0.02
	Sucrose	16.95 ± 1.36	17.99 ± 1.47	1.04 ± 2.01	0.52
	Starch	38.91 ± 0.36	37.77 ± 1.16	1.14 ± 1.21	0.94

When considered in proportionate relationships with each other, the mean values for reducing sugars were almost identical in both series of plants and the balance of difference was held by slightly higher sucrose and slightly lower starch in the diseased leaves.

The main direction of metabolism in the healthy leaves at this stage of development has been postulated to be that of carbohydrate formation and utilisation in tissue synthesis. During the day, when photosynthetic activity led to the formation of carbohydrate in excess of the needs in utilisation, it was shown that temporary storage products, starch and sucrose, were formed by condensation of reducing sugars whilst the reverse process of hydrolysis maintained the level of reducing sugars at night. The facts for the diseased laminae give support to this hypothesis and, therefore, the slight differences which have been noted must be ascribed to either an excess of utilisation or a diminished rate of formation of carbohydrate in these laminae. The fact that reducing sugars and starch were most markedly lower during the earlier part of the photosynthetic period/

period is suggestive of a lower rate of formation as the most probable explanation. Since the higher values of reducing sugars in the diseased laminae during the night may be taken to indicate that the demand made upon these sugars in support of respiration and synthesis was not as great as in the healthy laminae then the argument in favour of a lower rate of carbohydrate formation is considerably strengthened. The lag in time in starch fluctuations together with lower starch values on both actual and proportional bases lead to the further suggestion that starch formation is subject to additional impediment in the diseased laminae.

President Series 2. Age 44 days.

If the effect of virus infection is to decrease the efficiency of carbohydrate production, as indicated by the data for the young actively growing leaves, then stronger evidence of this diminished efficiency should be obtained when the trend of carbohydrate metabolism in the leaf is directed towards the formation of storage carbohydrates.

TABLE/

TABLE 2.

MEAN VALUES		HEALTHY	MOSAIC	DIFFERENCE	D/E_d
% R.D.W.	Red. Sugs.	0.564 ± 0·061	0.464 ± 0·066	0.100 ± 0·090	1.11
	Sucrose	1.780 ± 0.152	1.601 ± 0.166	0.179 ± 0.225	0.80
	Starch	1.636 ± 0.072	1.434 ± 0.081	0.202 ± 0.108	1.87
% Total	Red. Sugs.	14.42 ± 1.64	13.63 ± 2.05	0.79 ± 2.63	0.30
	Sucrose	44.21 ± 3.15	44.71 ± 3.11	0.50 ± 4.43	0.11
	Starch	41.36 ± 2.02	41.66 ± 2.78	0.30 ± 3.44	0.10

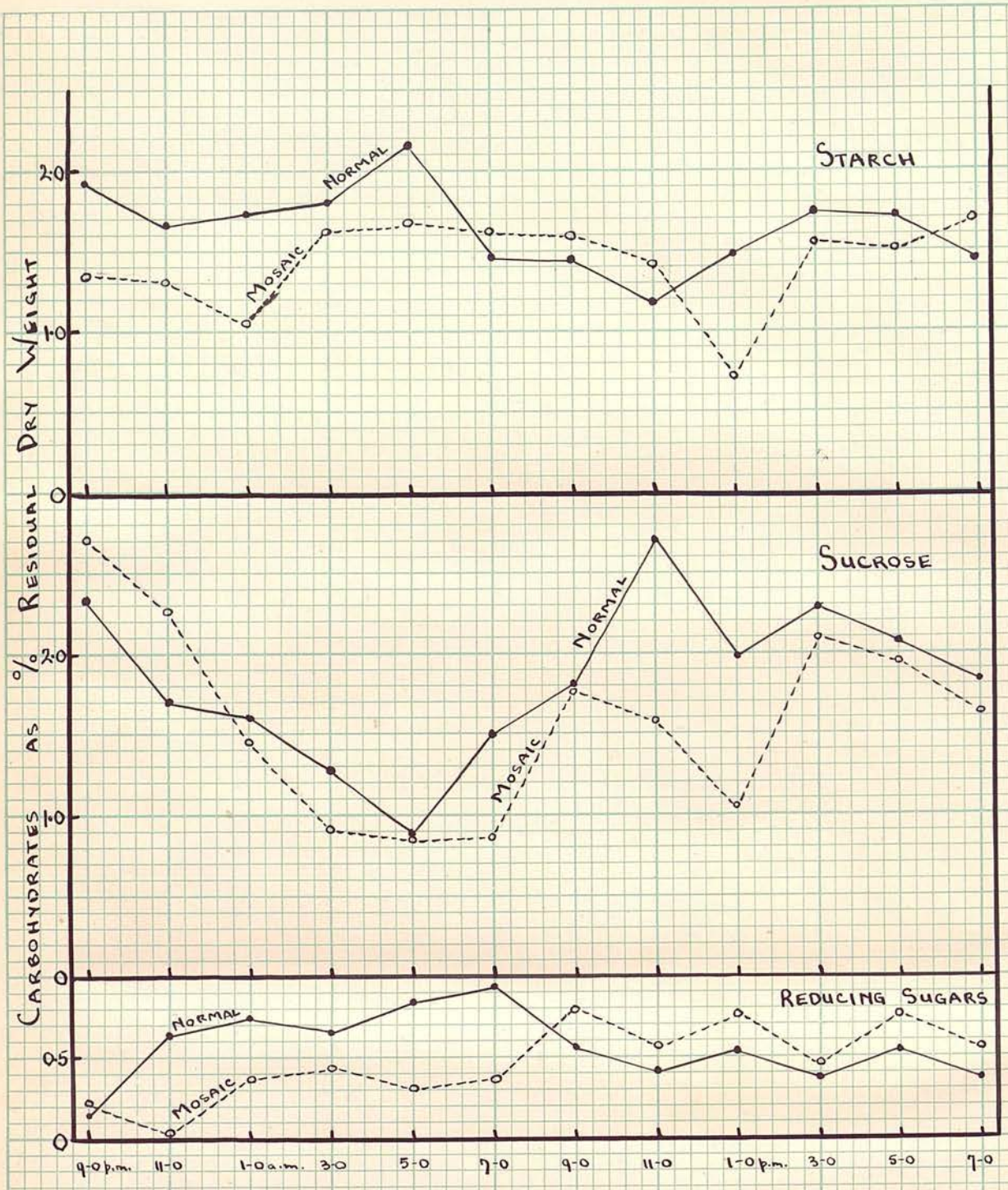

FIGURE 2. PRESIDENT SERIES 2. AGE 44 DAYS.
DIURNAL VARIATIONS IN CARBOHYDRATES OF NORMAL AND MOSAIC AFFECTED LEAVES.

The comparative mean values given in Table 2 support the presumption made above, for they show that in the second series of President all three forms of carbohydrate were lower in the diseased laminae. This general reduction in carbohydrate was not, however, the only difference between the two series as will be observed by comparing the curves for reducing sugars given in Figure 2. These curves show clearly that during the photosynthetic period, between 7.0 a.m. and 7.0 p.m., reducing sugars were of relatively greater values in the diseased laminae and tended to accumulate. On the other hand, an opposing tendency towards lower values during the night is also shown.

These differences in fluctuation of reducing sugars are quite the reverse of those found in President Series 1 and their interpretation must be sought in the light of the differences in seasonal metabolism between the leaves of President Series 2 and those of President Series 1. In the latter series the products of photosynthesis were found to be directed mainly towards utilisation in tissue synthesis and reducing sugars, i.e. the basic carbohydrates of this synthesis, predominated in the leaf. Disturbances in metabolism were reflected directly in the fluctuations of reducing sugars and the fact that/

that these latter were of smaller values during the day and tended to be of greater values during the night in the diseased leaves has been taken to indicate that they were formed to a less extent in photosynthesis and utilised to a less extent in general synthesis. In President Series 2, however, the picture of metabolism drawn from the carbohydrate relations of the healthy leaf was quite different. The leaves in this case were considered to function primarily as photosynthetic organs and the prevailing trend of metabolic activity was found in the formation and accumulation of carbohydrate reserves. Sucrose and starch were shown to serve as temporary storage products and to predominate over reducing sugars. Consequently, and as in President Series 1, disturbances in metabolism should be most readily observed in the direct line of synthesis, that is, in the synthesis of sucrose and starch. The enhanced values of reducing sugars in the diseased leaves during the photosynthetic period is not interpreted as indicative of an increased rate of carbon assimilation, therefore, but as a reduced rate of formation of sucrose and starch, since these latter are of lower values in the diseased leaves. Conversely, the lower values of reducing sugars during the night may be used as evidence/

evidence that the demand for these sugars in utilisation was greater than the supply available by hydrolysis of the temporary reserves and hence that the lower values were brought about by an impeded rate of hydrolysis of starch and/or sucrose. Since the starch fluctuations in the diseased leaves were not as great as those in the healthy leaves whereas fluctuations in sucrose, particularly during the night, were greater in the diseased leaves it would seem that the disturbed relationships were primarily those between reducing sugars and starch.

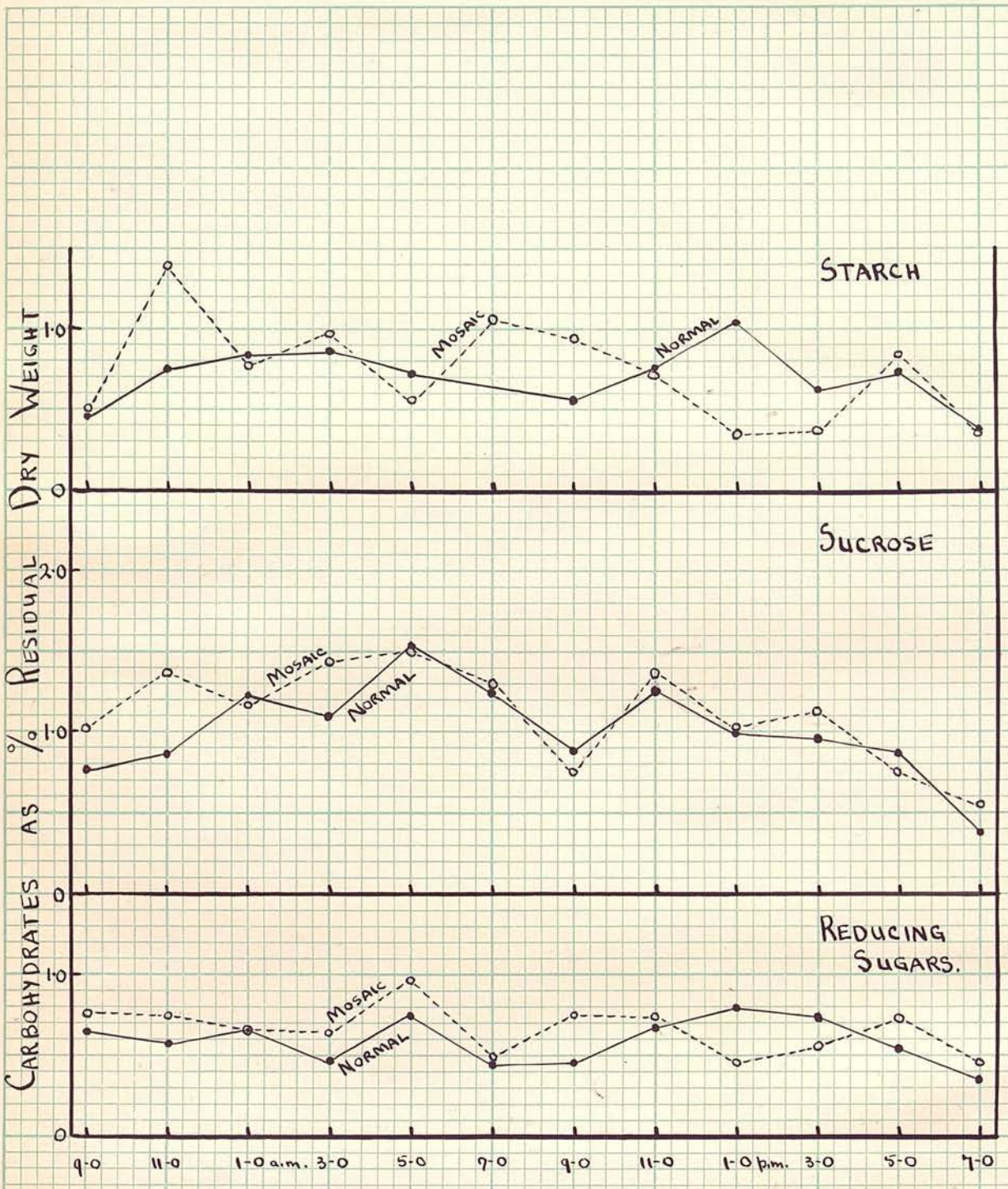

FIGURE 3. PRESIDENT SERIES 3: AGE: 86 DAYS.
DIURNAL VARIATIONS IN CARBOHYDRATES OF
NORMAL AND MOSAIC AFFECTED LEAVES.

President Series 3. Age 86 days.

The material for President Series 3 was obtained from plants which had reached a stage of growth immediately preceeding the onset of visible senescence. The comparative curves for the two series, Figure 3, show that both forms of soluble sugar fluctuated in similar fashion over the diurnal period but that starch, on the other hand, fluctuated more inconsistently with time in the diseased laminae.

TABLE/

TABLE 3.

MEAN VALUES			HEALTHY	MOSAIC	DIFFERENCE	D/Ed
LAMINA	% R.D.W.	Red. Sugs.	0.594 ± 0.039	0.666 ± 0.046	0.072 ± 0.060	1.20
		Sucrose	1.011 ± 0.082	1.120 ± 0.083	0.109 ± 0.117	0.93
		Starch	0.801 ± 0.107	0.739 ± 0.092	0.062 ± 0.141	0.44
	% Total	Red. Sugs.	25.55 ± 1.67	26.94 ± 1.44	1.39 ± 2.21	0.63
		Sucrose	41.82 ± 1.48	44.40 ± 2.25	2.58 ± 2.70	0.96
		Starch	32.54 ± 2.11	28.42 ± 2.34	4.12 ± 3.15	1.31
PETIOLE	% R.D.W.	Red. Sugs.	2.689 ± 0.234	1.505 ± 0.112	1.184 ± 0.259	4.57 *
		Sucrose	1.060 ± 0.270	0.946 ± 0.092	0.114 ± 0.285	0.40
		Starch	1.086 ± 0.102	0.909 ± 0.041	0.177 ± 0.110	1.61

* Significant difference

When the differences in carbohydrate levels, Table 3, are compared with those for President Series 2, Table 2, it will be seen that the differences in soluble sugars were reversed. Both forms of sugar were of higher values in the diseased laminae of President Series 3, whilst starch values, although lower, were appreciably nearer those of the healthy leaves. There was, therefore, a tendency towards a relative accumulation of all three carbohydrates in the diseased leaves. This finding is of particular interest since it corroborates the observations of BARTON WRIGHT and McBAIN (1933) and STONE (1936) for the maturing leaves of mosaic diseased potatoes.

It has already been suggested that the metabolism of the healthy leaf at this stage of growth was directed chiefly towards the breakdown of reserve carbohydrates and transport of soluble sugars to the tubers. In these circumstances an accelerated rate in the hydrolysis of reserve carbohydrate and/or a retarded rate of transport would lead to accumulation of soluble sugars and starch. Of these alternatives the latter lends itself to examination. By reference to the data for/

for the petioles given in Table 3 it will be seen that reducing sugars in the diseased material were lower than those in the healthy by an amount which reached statistical significance. Since reducing sugars have been considered to be the chief sugars of transport at this late stage of growth it would seem that there is an interference with translocation and that this alone offers a sufficient explanation of the observed facts. This again is corroborative of the findings of BARTON WRIGHT and MCBAIN (1933).

The alternative possibility, that the accumulation of the three carbohydrates is due to an accelerated rate of hydrolysis, is not disproved by this result but it is considered unlikely, nevertheless. It has already been indicated that synthetic activities in the diseased leaves are impeded and hence, since the mechanism of hydrolysis is presumably the same as that of synthesis, it would be expected that hydrolysis would be retarded and not accelerated. Furthermore, a concomitant of an increased rate of production of soluble sugars by hydrolysis should be found in an increased rate of removal. The data are not in accord with this supposition and therefore there are no grounds for assuming an accelerated rate of hydrolysis.

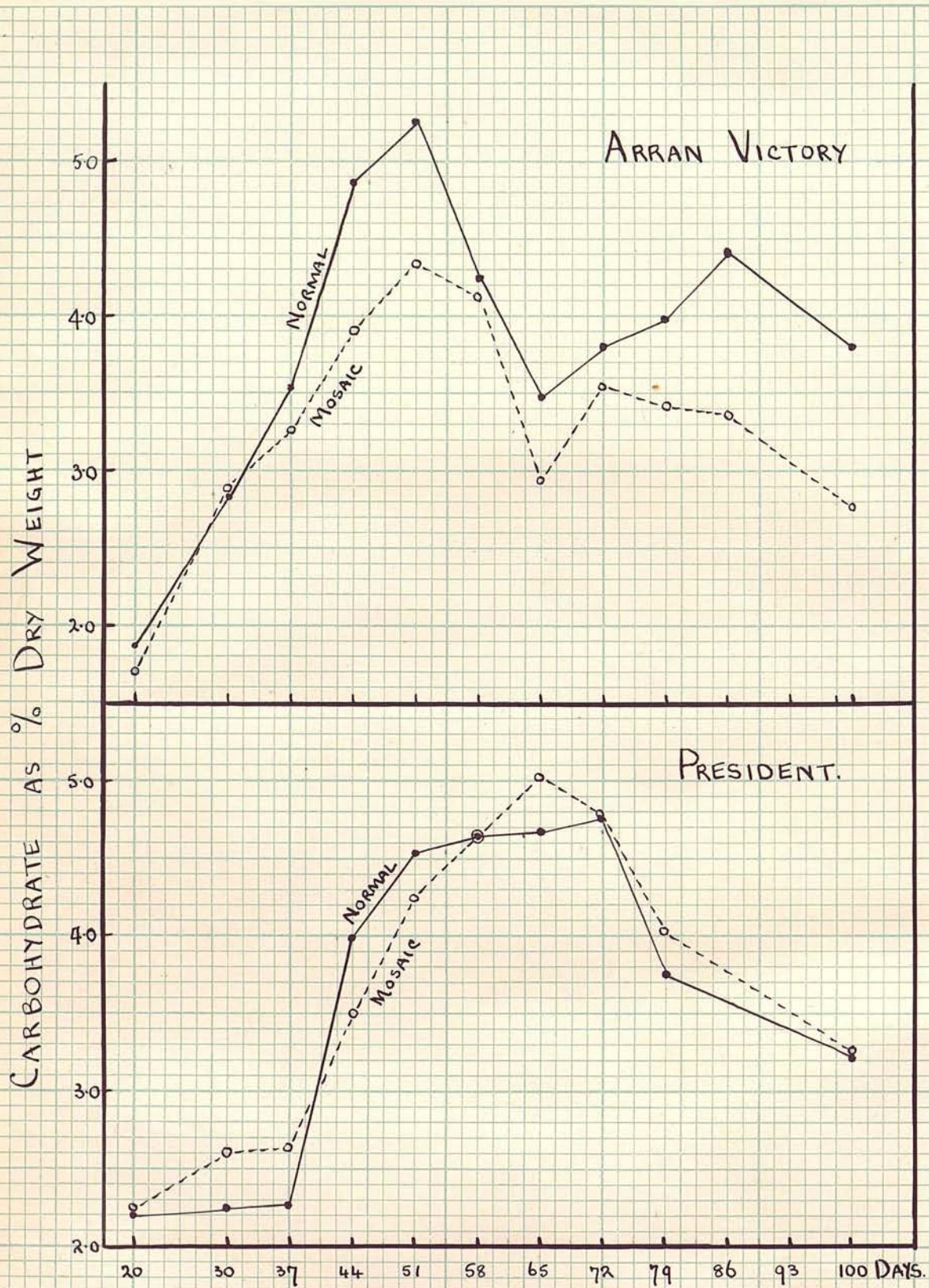

FIGURE 4. SEASONAL VARIATIONS IN TOTAL CARBOHYDRATES OF NORMAL AND MOSAIC AFFECTED LEAVES.

Seasonal variations in carbohydrates.

As in the case of the diurnal data, similarity is the most striking feature of the curves showing seasonal variations in the total carbohydrates of the healthy and diseased leaves. There are slight differences between the comparable curves, however, and an examination of these will serve to strengthen the various suggestions which have been made in considering the differences observed in diurnal metabolism.

An inspection of the curves for both President and Arran Victory (Figure 4) reveals a slight tendency towards lower carbohydrates in the diseased leaves at 20 days. A little later the curves cross over and that for the diseased leaves rises above the curve for the healthy leaves. This appears to be a transient phase, however, and the curves again cross and show that carbohydrate values of the diseased leaves remained lower than those of the healthy during the greater part of the period of carbohydrate accumulation.

It has been suggested that in the healthy leaf the seasonal trend of metabolism during the earlier stages of growth was determined chiefly by the relationship between the function of the leaf as/

as a photosynthetic organ and its requirements as a growing organ. At 20 days there appeared to be a balance between the two by which the requirements of the leaf were supplied, but not to excess, by photosynthetic activity. Later, however, the requirements in growth were relatively lessened, the balance was destroyed and carbohydrate formation exceeded the rate of utilisation with the result that storage products were formed in increasing quantity. Since the gross metabolism of the diseased leaves appears to be similar to that of the healthy then the enhanced values of carbohydrate in the diseased leaves at 30 days would seem to be due to a relatively large decrease in the requirements of the leaf as a growing organ. In other words, the growth activities of the leaf would appear to be considerably diminished. In the normal course of events this would lead to increased values of sucrose and starch. The mean values for Arran Victory Series 1, Table 4, show that actually the greatest increases in the diseased leaves at this stage occurred in soluble sugars, including reducing sugars. The discrepancy is readily explained, however on the basis/

basis that starch formation in the diseased leaves was impeded and that in consequence there was a corresponding increase in reducing sugars and sucrose.

TABLE/

TABLE 4.

MEAN VALUES		HEALTHY	MOSAIC	DIFFERENCE	D/E_d
% R.D.W.	Red. Sugs.	0.407 ± 0.055	0.648 ± 0.064	0.241 ± 0.084	2.87
	Sucrose	1.416 ± 0.066	1.613 ± 0.056	0.197 ± 0.087	2.26
	Starch	0.803 ± 0.032	0.723 ± 0.045	0.080 ± 0.055	1.46
% Total	Red. Sugs.	15.06 ± 1.67	21.47 ± 1.87	6.41 ± 2.51	2.56
	Sucrose	53.92 ± 1.40	55.12 ± 1.93	1.20 ± 2.39	0.50
	Starch	31.02 ± 1.57	23.86 ± 2.23	7.16 ± 2.73	2.62

It would appear from the curves that growth of the healthy leaves, as measured by carbohydrate requirements, took place over a longer period than that of the diseased leaves. When growth was eventually retarded and the balance between carbohydrate formation and its utilisation destroyed, accumulation would appear to have taken place to a more rapid extent in the healthy leaves with the result that the seasonal curves again show a cross over. This points again to a reduced efficiency in carbon assimilation in the diseased leaves. It is of interest to recall, therefore, that although the only metabolic disturbances traceable in the second diurnal investigation of President, representative of the period, were those relative to formation and hydrolysis of the temporary storage products, the mean diurnal value of each carbohydrate was lower in the diseased laminae.

The further rise in the seasonal carbohydrate levels of President is again followed by a cross over in the curves at 58 days. No diurnal data are available for this period, however,and there is no direct evidence therefore upon which to establish the cause of the reversal. Since there is no reason for/

for assuming that photosynthetic activities became more efficient in the diseased laminae, it would seem probable that diminished utilisation may be responsible for the relatively greater carbohydrate values. The development of flowers at this stage may have a bearing on the differential utilisation of carbohydrate in the two series, for there is evidence that flower production in diseased plants is reduced. It will be shown later that the carbohydrate/nitrogen relationships in diseased plants are affected to a great extent by an increase in nitrogen and it is entirely possible therefore to ascribe the reduction in flowering capacity to the lower C/N ratio and the accumulation of carbohydrate to a lessened demand in the maintenance of growth and development of flowers.

Carbohydrate relations during the period of depletion have been examined in some detail during a consideration of the diurnal investigation of President Series 3. It was then found that relatively enhanced values of carbohydrate in the diseased leaves were ascribable, in part at least, to a diminished rate of transport. The seasonal curves fully corroborate the fact of a relative accumulation of carbohydrate/

carbohydrate over the whole of this period although they throw no further light on the cause of accumulation. If the seasonal curves for Arran Victory are now examined it will be seen that after the transient reversal in carbohydrate values by a retardation of growth activities in the earlier part of the season, the production of carbohydrate in the diseased leaves was considerably impeded and relatively smaller amounts were formed at all subsequent stages of growth. Furthermore, the response to manurial treatment, described in considering the healthy material, was apparently greater and was maintained over a longer period in the healthy leaves than in the diseased with the result that differences in carbohydrate content widened considerably towards the end of the season.

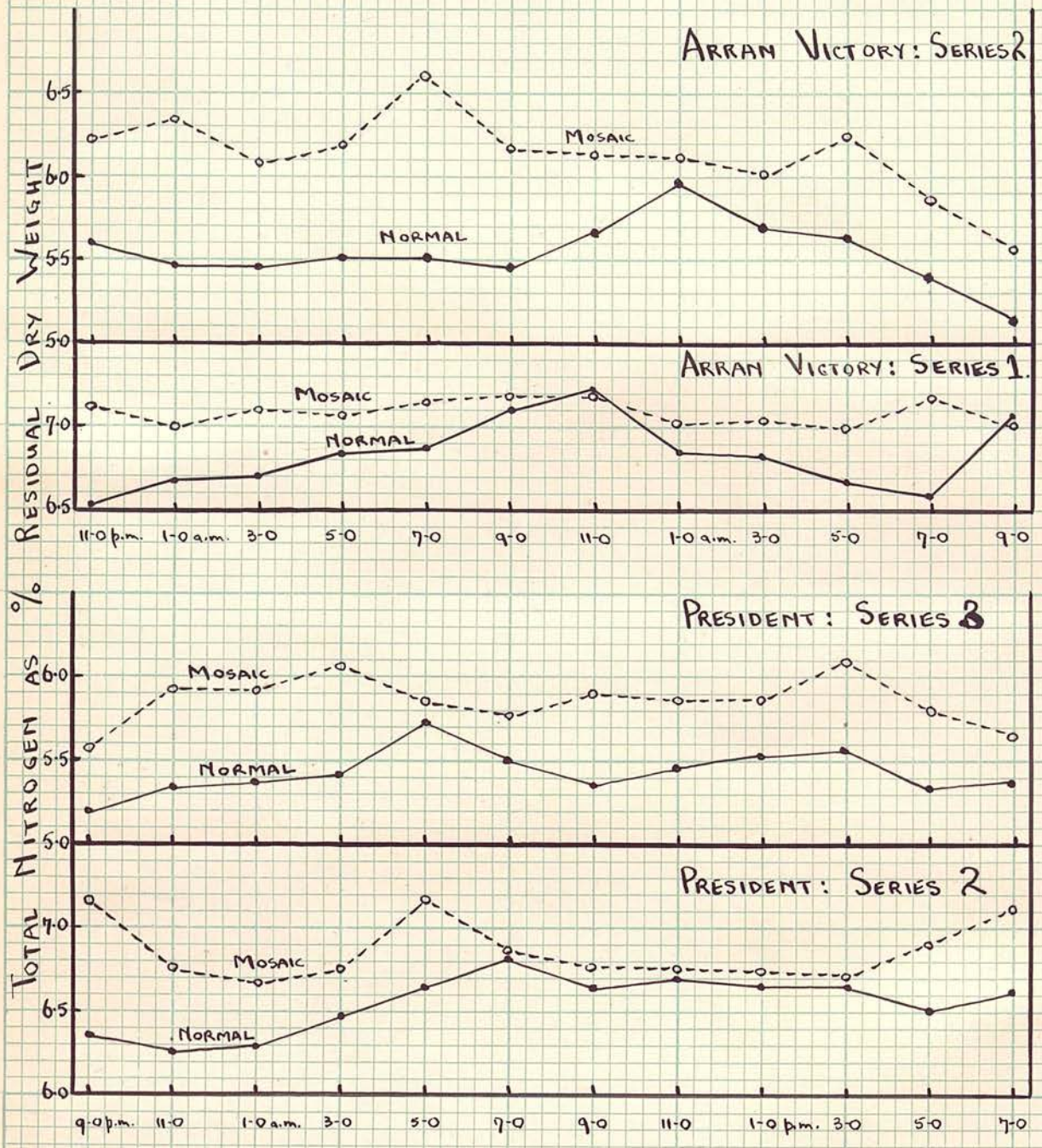

FIGURE 5. DIURNAL VARIATIONS IN TOTAL NITROGEN OF NORMAL AND MOSAIC AFFECTED LEAVES.

Total Nitrogen.

The comparative curves showing diurnal and seasonal variations in the total nitrogen content of healthy and mosaic infected leaves of both President and Arran Victory are given in Figures 5 and 6. Two significant facts are immediately observable on inspection of the curves. Firstly, it is evident that total nitrogen was greater at all times in the diseased leaves; and secondly, there was but little difference in the trend of variation either in diurnal or seasonal time. The greater differences are to be seen in the diurnal curves but as no data are available for the various nitrogen fractions the possible significance of these differences cannot be estimated.

TABLE/

TABLE 5.

	SERIES	HEALTHY	MOSAIC	DIFFERENCE	D/E_d
Total N as % of R.D.W.	Pres. 1	6.555 ± 0.047	6.875 ± 0.051	0.320 ± 0.069	4.64 *
	A. Vic.1	6.829 ± 0.060	7.090 ± 0.022	0.261 ± 0.064	4.08 *
	A. Vic.2	5.546 ± 0.056	6.138 ± 0.069	0.592 ± 0.107	5.53 *
	Pres. 2	5.435 ± 0.037	5.867 ± 0.040	0.432 ± 0.055	7.85 *

* Significant differences.

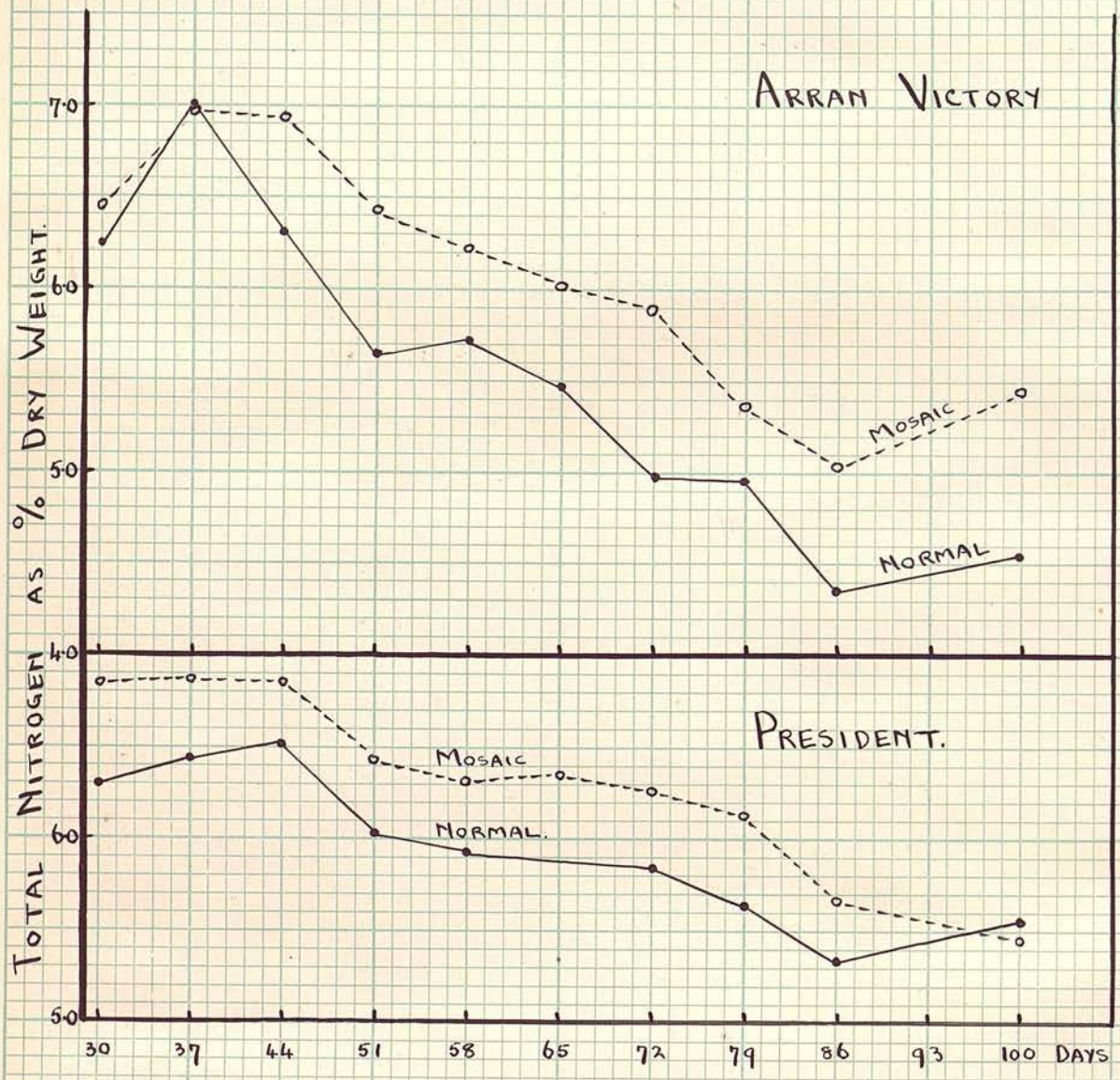

FIGURE 6. SEASONAL VARIATIONS IN TOTAL NITROGEN OF NORMAL AND MOSAIC AFFECTED LEAVES.

The mean diurnal values for each of the four periods of investigation are given in Table 5. The differences between the healthy and the diseased series show a marked tendency to widen with increase in age of the leaves and with decrease in the amount of nitrogen. In all cases, however, the differences are sufficiently great to reach a high degree of statistical significance.

DISCUSSION.

It has already been emphasised that the comparison between carbohydrate variations, over both diurnal and seasonal periods, has established a similarity in the gross metabolism of carbohydrates of both normal and mosaic infected potato leaves. Nevertheless, a detailed examination of the data has provided evidence that modifications of the fundamental metabolism, slight though definite in character, may arise in consequence of mosaic infection. It will be recalled that at each stage of diurnal investigation there were lower starch values in the diseased laminae and that slight but noticeable differences in carbohydrate variation pointed constantly towards impediment in starch formation and hydrolysis. In addition, there was indication of an interference with the utilisation of sugars during the early stages of growth when the leaves were actively engaged in tissue synthesis. This interference in utilisation became very pronounced a little later and it was suggested that the cause was to be found in a premature retardation of growth activities which was reflected in the diversion of the/

the products of photosynthesis from utilisation in tissue synthesis to the formation of storage carbohydrates. This change in metabolism proceeded in normal fashion and merely anticipated a similar change in the healthy leaf. The difference in trend of metabolism between the two series was, moreover, quite transient and subsequently the only differences to be found were in slightly reduced amounts of carbohydrate and in the persistent interference with starch elaboration in the diseased leaves.

A further apparent disturbance was noted during the flowering period of growth in President but again, though there was no direct evidence, the cause was sought not in carbohydrate metabolism *per se* but more probably in its relation with nitrogen metabolism. During the post-flowering and pre-senescent stages of growth an interference with translocation became evident. In consequence there was a slight disorganisation in metabolism due to accumulation of soluble sugars, but no trace was found of any large interference with the normal processes of carbohydrate degradation characteristic of the period.

The causation of these differences in the carbohydrate economy of mosaic infected leaves as compared/

compared with healthy leaves may be sought therefore in two possible sources. In the first place, the slightly reduced efficiency in carbon assimilation, the disturbed starch-sugar relationships and the impeded translocation may be traced directly to the pathological changes brought about by the virus. SMITH (1924) and CLINCH (1931) have made anatomical studies of potato leaves affected with mosaic diseases and their observations show that histopathological symptoms within potato leaves affected with mild or simple mosaic are, in general, restricted to the mottled areas. In these areas the mesophyll is undeveloped, there is a reduction in size and number of chloroplasts and the chlorophyll has a paler appearance. Clinch has shown further that the extent of these modifications is proportional to the external visible symptoms of the disease and that there are marked abnormalities in the starch content of cells in the chlorotic areas. ROCHLIN (1930) has provided evidence, in contrast with that of the above authors, to show that pathological symptoms consequent upon infection with mosaic viruses are not restricted to the mottled areas, but may spread to destructive changes in the conducting tissues. Again, however, her conclusions

are/

are qualified by the observation that the extent of internal symptoms is correlated with the severity of the external symptoms visible upon the leaves.

Since the disease symptoms upon the leaves of the potato varieties used in the present investigation were confined to small, slightly chlorotic, mottled areas, and in view of the anatomical evidence, the slight disturbances which have been observed in diurnal carbohydrate metabolism would appear to be directly associated with presence of the mottled areas. It would seem, indeed, that the greater portion of the leaf surface functions quite normally with regard to the formation and utilisation of sugars but that in the relatively small areas in which pathological symptoms are manifested the formation of sugars in photosynthesis does not take place, or takes place to a small extent only, and the formation and degradation of starch are subject to impediment. This conclusion is in entire agreement with that of COOK (1926) who has shown that in sugar cane the green areas of mosaic infected plants synthesise sugars in the normal manner but that the products of photosynthesis, particularly starch, are reduced in proportion to the amount of visible infection.

The interference with translocation towards the/

the end of the season may similarly be ascribed to pathological changes in the light of ROCHLIN'S evidence but in the absence of specific data upon the channels of translocation by which reducing sugars are removed from the leaves, no great stress can be laid upon this suggestion.

A second cause of modification in the carbohydrate metabolism of mosaic infected leaves has been traced to disturbances affecting primarily the growth activities of the plant. Thus in the early stages of development indication was obtained that growth was retarded in the diseased leaf earlier than in the healthy leaf. During the flowering stage also there was indication that carbohydrate was not used in the support of flower production in the diseased plant to the same extent as in the healthy plant. There has been no evidence to suggest, however, that the disturbances in carbohydrate metabolism were the causes of these interferences with growth. It would seem, indeed, that the cause must be found in some other aspect of the general metabolism. In this connection the results of the nitrogen analyses are of considerable interest since they show that the total nitrogen content of diseased leaves is affected to

a/

a relatively greater extent than the carbohydrate content. It may be, therefore, that the pathological symptoms and retarded growth activities which give rise to disturbances in carbohydrate metabolism are direct manifestations of a disorganised nitrogen metabolism.

SUMMARY.

(1) The effect of a mosaic virus upon the carbohydrate relationships and upon the total nitrogen content of potato leaves has been followed over diurnal and seasonal periods in the potato varieties President and Arran Victory.

(2) The gross metabolism of carbohydrates in both mosaic infected and normal leaves has been found to be similar.

(3) Slight modifications of the fundamental metabolism have been found in disturbed starch-sugar relationships and these together with a reduction in the photo-synthetic activity of the leaf and an impediment in translocation in the post-flowering stages of growth have been ascribed to secondary effects arising out of the pathological changes brought about as a result of virus infection.

(4) Further transient modifications in seasonal carbohydrate metabolism have been traced to retarded growth activities leading to a diminished demand for carbohydrate in support of growth in the diseased plants.

5/

(5) A significantly greater content of total nitrogen has been found in diseased leaves at all stages of growth and it has been suggested that the pathological symptoms and retarded growth activities which give rise to disturbances in carbohydrate metabolism are direct manifestations of a disorganised nitrogen metabolism.

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SECTION II

A Study of the Effects of Virus Diseases upon Yield and Reproduction in the Potato.

C O N T E N T S

INTRODUCTION

Investigation into the pathological effects of virus diseases upon flower and fruit production have been confined almost entirely to ornamental species in which flowers are of prime importance and to economic species in which fruit and seed constitute the crop. Surveys of the literature on these various effects have been made by HEALD (1926) and SMITH (1933). So far as the present writer is aware, no previous study has been made of virus diseases in relation to their effects upon sexual reproduction in the potato. Diminished numbers of flowers in affected plants have been recorded by AITKEN (1837), ANON (1925) and USPENSKY and premature abscission of flowers in mosaic diseased potatoes by HEALD (1926) but in no case was attempt made either to evaluate the extent of reduction or to trace its causes. In the related genus Nicotiana, however, KOSTOFF (1933a, 1933b) has examined in detail marked cases of abnormality in flower production in plants affected with virus diseases and has concluded that the causes are physiological in origin and may result not only in abnormalities in floral parts and reproductive organs but also in disturbances in the reproductive/

reproductive processes.

With regard to asexual reproduction there are numerous accounts of reductions in yield of tubers following infection with virus diseases but the data have been obtained almost entirely from comparisons between poor stocks of potatoes, in which there was a large proportion of diseased plants, and stocks derived from commercially good but not necessarily disease-free seed. There appear to be no data, other than very general estimates, relative to the comparative effects of individual viruses upon yield nor are there comparisons between varieties in respect of the reductions in yield brought about by similar diseases.

The objects of the present study are to compare the effects of different viruses upon vigour, as measured by the flowering and cropping capacities of individual varieties; to compare similar diseases in their effects upon the cropping capacities of "susceptible" and "resistant" varieties; and to obtain an insight into the nature of the effects of virus infection upon flower and fruit formation in the potato.

MATERIAL

The six varieties of potatoes used as experimental material were selected in three pairs of similar maturity, one member of each pair being relatively susceptible and the other relatively resistant to the effects of virus diseases as judged by previous observational estimates of vigour. The varieties selected and the diseases with which each was infected are summarised in the following table.

TABLE 1

Maturity	Susceptible	Resistant	Disease	Virus
Early	Alness	Di Vernon	Leaf roll	LR
Early Maincrop	Majestic	Great Scot	Leaf roll	LR
Maincrop	President	Arran Victory	Leaf roll	LR
do.	do.	do.	Mosaic (mild)	X
do.	do.	do.	Mosaic (severe)	Y
do.	do.	do.	Crinkle	A + X

The basic stocks of Alness, Di Vernon, Majestic and Great Scot were derived from tubers certified/

certified in 1935 as "Stock Seed" by the Department of Agriculture for Scotland. In the year of trial the healthy controls of each of these varieties proved to be free from visible symptoms of virus disease and remained free throughout the season. The controls for President and Arran Victory were grown from seed of "T.S.H." grade and, as was expected, a trace of mild mosaic was found among them. This presence of disease has been ignored in formulating the results as the diseased plants were few in number and were affected to a slight extent only. The source of diseased material in the case of Alness, Di Vernon, Great Scot and Majestic was the basic stock described above and infected in the year of trial. The diseased material of President and Arran Victory was obtained from plants previously infected and raised under conditions of isolation in the greenhouse.

METHODS

In January 1936, 180 tubers of each of the varieties Alness, Di Vernon, Great Scot and Majestic were selected for equality of size and divided into three groups of 60 tubers. Each group was planted in shallow boxes and sprouted. When the sprouts were 1-1½ inches in length aphides, Myzus persicae SULZ., previously fed on leaf roll infected plants of Arran Victory, were introduced on to the sprouts of one group and other aphides, previously fed on Arran Victory with virus Y, were placed on the sprouts of a second group. The third group was infested with virus-free aphides cultured on radish. After 20 days feeding the aphides were killed with a nicotine fumigant. Almost 100% of the tubers upon which had been placed insects from the leaf roll plants contracted this disease but not a single tuber of the second group became infected with the Y virus. This latter result is inexplicable as it is well known that Myzus persicae is an efficient vector of virus Y, (SMITH 1931). In all respects other than infestation with aphides the various groups of healthy and diseased tubers of President and Arran Victory were treated in identical manner as those of the/

the remaining four varieties.

The original trial was laid down in the form of a threefold 6 x 6 Latin Square, one for each maturity group, with 10 tubers in each replication. A plan of the arrangement is given in Figure 1. As no Y virus was transmitted in sprout infection the plots of Alness, Di Vernon, Great Scot and Majestic reserved for this virus contained healthy plants. These plots were eliminated in calculating the results and in consequence the Latin Square arrangement was reduced to one of randomised blocks in which each unit of comparison was represented by 60 tubers in 6 replicate blocks of 10 tubers.

All the tubers were planted on 23rd April 1936 and the plants were harvested on 1st October. When harvested the healthy and diseased plants of Alness, Di Vernon, Great Scot and Majestic and the diseased plants of President and Arran Victory were fully mature but the healthy plants of the latter varieties were merely beginning to mature at this time. The produce of each individual plant was weighed when lifted and the analyses of yield have been based on the aggregate weight of tubers in each plot. The data have been subjected to statistical treatment as suggested by FISHER and WISHART (1930)/

(1930) for randomised plots. In one instance, Di Vernon variety, it was necessary to apply the method of estimating the yield of a missing plot, ALLAN and WISHART (1930), in order to compensate for tubers which remained uninfected after sprout feeding with infective aphides.

The number of flower trusses, flower buds, persistent flowers and berries were counted throughout the whole season on plants of the varieties President and Majestic selected at random during the early stages of growth. These data have been analysed by the methods given by FISHER (1932). In the tables relative to these latter analyses the following abbreviations have been used.

H = healthy. LR = leaf roll

X = mild mosaic caused by virus X.

Y = severe mosaic caused by virus Y.

A + X = crinkle caused by the complex A + X.

M = mean. SE_M = standard error of mean.

SD = standard deviation.

SE_σ = standard error of standard deviation.

D = difference between the values for the diseased plants and those for the healthy plants.

E_D = standard error of difference.

D/

D/E_D = the ratio between the observed difference and its standard error. This ratio is a measure of significance and is related to the number of samples, $n_1 + n_2$, in the two comparable populations.

P = the maximum probability that the observed difference is due entirely to accident. If $P < 0.01$ then the difference is considered to be of full statistical significance.

EXPERIMENTAL RESULTS

A. The effect of virus diseases on yield.

The data relative to the yields of the various healthy and diseased groups of plants have been treated in such a manner as to compare variety and health of variety in each maturity group. The details of these analyses are given fully in Appendix Tables 2-4 and for convenience of reference a summary of the results is included in Table 5 below. In this Table the mean yield is given in terms of lbs. per plant and the mean reduction caused by virus infection as the difference between the yield of the diseased plant and that of the healthy control. Since the mean yields of the healthy plants of two comparable varieties differ considerably in some cases, the reduction in yield has also been calculated as a percentage of the yield of the healthy control in order to facilitate comparison.

TABLE/

TABLE 5

VARIETY	CONDITION	YIELD	REDUCTION	
			lbs.	%
Alness	H	2.3241	-	-
	LR	0.6802	1.6439*	70.73*
Di	H	2.8697	-	-
Vernon	LR	1.1159	1.7098*	59.58*
Majestic	H	3.8699	-	-
	LR	1.5689	2.3010*	59.46*
Great	H	3.7989	-	-
Scot	LR	2.0768	1.7221*	45.33*
President	H	3.2740	-	-
	LR	0.1445	3.1295*	95.61*
	X	3.1797	0.0943	2.88
	A + X	1.0871	2.1869*	66.82*
	Y	1.0278	2.2462*	68.61*
Arran	H	4.2144	-	-
Victory	LR	1.6990	2.5154*	59.69*
	X	3.5769	0.6375	15.12
	A + X	2.2829	1.9315*	45.84*
	Y	2.3384	1.8760*	44.51*

*Significant difference.

By/

By inspection of the summarised data it is evident that the effect of leaf roll upon each of the six varieties was to reduce the yield of tubers to a large and statistically significant extent and, also, that within each maturity group the reduction, calculated as a percentage of the mean yield of the healthy controls, was greater for the "susceptible" variety. Furthermore, if the varieties are arranged in order of the relative and increasing reduction in yield thus, Great Scot 45.33%, Di Vernon, Majestic and Arran Victory, 59.58%, 59.46% and 59.69% respectively, Alness 70.73% and President 95.61%, it is possible to suggest that this order indicates the relative and increasing effect of the leaf roll virus upon the vigour, as measured by yield, of the six varieties.

The effects of the mosaic viruses were ascertained in the varieties President and Arran Victory only. The summarised data show that in both these varieties the reduction in yield brought about by infection with virus Y or the crinkle complex A + X was great and statistically significant but, nevertheless, was less than that brought about by leaf roll. The reduction due to virus X was small and statistically insignificant in both varieties.

The/

The similarity in extent of reduction caused by virus Y and the complex A + X was not unexpected since the diseases manifested upon the two varieties by each pathogen can be described in general terms as severe mosaics although the detailed symptoms are quite different.

With regard to the differential varietal response, it is clear that the reductions due to leaf roll and the severe mosaics were greater in President than in Arran Victory but that reduction due to virus X was slightly greater in the latter variety.

B. <u>The effects of virus diseases upon flower and fruit formation</u>.

It has previously been stated that in addition to the estimation of yield as a measure of the effects of virus diseases on vigour the mean numbers per plant of flower trusses, flower buds, persistent flowers and berries have been counted in the variety President affected with X, A + X, Y and leaf roll viruses and also in Majestic affected with leaf roll. These various data are given in Appendix Tables 6-9 and are summarised in Table 10 below.

TABLE/

TABLE 10

VARIETY	CON-DITION		YIELD	TRUSSES	BUDS	FLOWERS	BERRIES
PRESIDENT	H	M	3.27	19.25	255	178	15.6
	X	M	3.18	17.50	214	104	18.0
		D	0.09	1.75	41	74	2.4
	A+X	M	1.09	10.00	127	39	3.4
		D	2.19*	9.25*	128*	139*	12.3*
	Y	M	1.03	3.73	41	10	1.4
		D	2.25*	15.52*	213*	167*	14.2*
	LR	M	0.14	11.23	138	90	8.6
		D	3.13*	8.02*	117*	88*	7.0*
MAJESTIC	H	M	3.87	11.95	110	55	7.9
	LR	M	1.57	7.00	65	37	4.9
		D	2.30*	4.95*	45*	18*	2.3*

*Significant difference

Clearly from the summarised values, each of the diseases affected flower and fruit formation through reductions in the number of trusses, buds, flowers and berries. The reductions were, moreover, large and of statistical significance in the cases of the severe mosaic and leaf roll diseases but small and insignificant in the case of mild mosaic due/

due to infection with virus X.

The question now arises as to whether these reductions were due solely to affected vigour or whether they were brought about by other causes in addition. The fact that in every case there was a reduction in the number of flower trusses, upon which the numbers of buds, flowers and berries are strongly dependent, is suggestive that limitations in truss formation were at least partly responsible for the generally diminished flowering capacity. The decrease in numbers of trusses was not, however, parallel to that in yield as is strikingly evident from a comparison of the respective mean values.

Before examining this aspect of the general problem further, it is convenient to consider in more detail the effects of viruses on flower and fruit formation. For this purpose the data have been reassembled and analyses made of the numbers of buds, flowers and berries on the basis of a single truss. The analyses are given in Appendix Tables 11-13 and are summarised in Table 14. In this latter table two additional calculations are also given in order to express more clearly the comparative effects of the viruses upon persistence of flowers and upon fertility. Persistence of flowers has/

has been calculated by the ratio:

$$\frac{\text{number of persistent flowers}}{\text{number of buds}} \times 100$$

and fertility by the ratio:

$$\frac{\text{number of berries}}{\text{number of persistent flowers}} \times 100$$

TABLE 14

VARIETY	CON-DITION		BUDS	FLOWERS	PERSIST-ENCE	BERRIES	FERTIL-ITY
PRESIDENT	H	M	12.3	9.15	74.21	0.80	8.74
	X	M	12.2	7.30	59.85	1.12	15.34
		D	0.2	1.86*	-	0.32	-
	A+X	M	12.7	3.91	30.79	0.34	8.69
		D	0.4	5.24*	-	0.47*	-
	Y	M	11.1	2.74	24.71	0.36	13.14
		D	1.2*	6.42*	-	0.44*	6
	LR	M	12.5	8.08	64.10	0.78	9.65
		D	0.1	1.07*	-	0.03	-
MAJESTIC	H	M	9.2	4.55	49.35	0.66	14.51
	LR	M	9.2	5.34	57.85	0.71	13.29
		D	0.-	0.79*	-	0.05	-

*Significant difference

The observation recorded by HEALD (1926) that premature abscission of flowers accompanies mosaic infection is supported by the data in Table 14 which show that each of the mosaic viruses caused a highly significant reduction in the number of flowers persisting to maturity. Furthermore, the effect was more pronounced in plants affected with the severe mosaics than in those affected with mild mosaic.

It is of interest to note that the number of flower buds formed upon each truss was affected to a significant extent in one case only, that of virus Y, whilst the number of berries, though reduced to a significant extent by the severe mosaic diseases, was affected solely through lack of persistence of flowers. Fertility, indeed, appeared to be unaffected or even to be slightly greater in the diseased plants.

With regard to leaf roll, the numbers of buds and berries per truss were entirely unaffected by the disease. The effect of this disease upon the persistence of flowers was just significant in each variety but it is noteworthy that in President persistence was reduced slightly, whilst in Majestic the tendency was towards increase in persistence.

DISCUSSION

From the comparisons which have been made between the yields of potato plants infected with virus diseases and those of normal plants it may be concluded that decrease in yield is dependent upon two factors, namely, the nature of the disease manifested and the inherent constitution of the variety infected. The facts that within each of the two varieties President and Arran Victory leaf roll reduced the yield to the greatest extent, that the two severe mosaics reduced yield almost equally, and that mild mosaic caused only a slight and insignificant reduction, relates the yield to the disease rather than to the virus causing the disease.

In comparisons between varieties the reduction in yield caused by leaf roll was found to vary considerably in proportionate relationship with the yield of the corresponding normal plants but in each of the six varieties under trial the reduction was sufficiently great to be of high statistical significance. A similar varietal effect was found in respect of the two severe mosaics caused respectively by the A + X complex and the Y virus. Again, however, the depressions in yield in each of the two varieties concerned were large and of significant/

significant proportions. Because of these large reductions none of the varieties examined can be considered to have shown a high degree of resistance to the diseases under discussion. Nevertheless, the fact that the varieties differed considerably in their response to infection is sufficient evidence for the suggestion that there are present in those varieties which were least affected characters which may be considered to offer resistance to the disease in its effects upon the physiological relationships of the host plant.

The existence of evidence pointing to a positive form of resistance to virus infection is of outstanding importance to the potato breeder as it is possible that the factors concerned are hereditary and, therefore, that they are capable of segregation and intensification by suitable methods of breeding. This possibility will be considered further in a later discussion. (Section 3).

The effects of virus diseases upon reproductive capacity have been studied chiefly in the variety President. The data obtained fall naturally into two classes for purposes of discussion. In the first place, each disease examined has been found to be accompanied by a reduction in totall reproductive capacity/

capacity which has been traced primarily to diminished numbers of flower trusses. It has been indicated earlier, page 119, that the extent of reduction in number of trusses was not parallel to the reduction in yield. This is shown with greater clarity in Table 15 in which the various ratios between numbers of trusses and yield have been calculated.

TABLE 15

Trusses / Yield	PRESIDENT					MAJESTIC	
	H	X	A+X	Y	LR	H	LR
M	5.87	6.90	7.87	3.82	54.40	3.14	4.31
SE_M	0.37	0.39	0.63	0.42	5.26	0.18	0.48
SD	1.61	1.35	2.50	1.62	17.44	0.79	2.03
D	-	1.03	2.00	2.05	48.53	-	1.18
SE_D	-	0.54	0.73	0.56	5.27	-	0.51
D/E_D	-	1.92	2.75	3.67	9.21	-	2.01
$n_1 + n_2$	-	25	35	34	30	-	38
P	-	>0.05	<0.01	<0.01	<0.01	-	>0.02

It may be concluded from inspection of the ratios that each of the characters was affected independently, i.e. from the statistical but not necessarily from the physiological point of view, by the various/

various diseases. Further, it is evident that neither yield nor number of trusses can be used as an estimate of vigour representative of the whole plant. The most striking feature of the data is that with the exception of virus Y each virus caused a relatively greater reduction in yield than in the number of trusses. A possible explanation of this differential response to virus infection may be sought in a consideration of the effects of virus diseases upon some of the major factors affecting truss formation and yield.

In a normal plant of any one variety grown under any one set of conditions, it may reasonably be expected that the number of trusses and the number and weight of tubers, i.e. yield, would be dependent to an equivalent extent upon the number of stems and the number of internodes comprising each stem. In other words, both characters may be said to be equivalently dependent upon the number of units of shoot growth. Support for this conception is provided by the fact that <u>within</u> each group of plants used as experimental material the number of trusses was correlated in positive and significant fashion with the yield of individual plants. (Table 16).

TABLE/

TABLE 16

VARIETY	CONDITION	r. YT	n	P
PRESIDENT	Healthy	+ 0.93	19	< 0.01
	Leaf roll	+ 0.71	20	< 0.01
	X	+ 0.84	6	< 0.02
	Y	+ 0.66	15	< 0.01
	A + X	+ 0.88	.11	< 0.01
MAJESTIC	Healthy	+ 0.68	20	< 0.01
	Leaf roll	+ 0.71	20	< 0.01

It is necessary to explain, therefore, the differential effect of virus diseases on two related characters each of which is linked with a third. Factors affecting this third character, namely, units of shoot growth, may arise in two ways. Firstly, the number of units may be reduced or increased. In this case, both yield and numbers of trusses would be affected to an equivalent extent. Secondly, the size and/or efficiency of each unit may be affected, in which case the number of trusses would remain unaffected, although the size of each truss may be affected, but the yield would show a corresponding/

corresponding increase or decrease. In examining the effect of virus diseases upon plant vigour it is necessary, therefore, to discriminate between the effect on numbers of organs and the effect on size and efficiency of organs. There is evidence that both number and size are reduced by virus infection but that size is affected more greatly than number. Thus CALDWELL (1934) and STONE (1936) have demonstrated, each in different fashion, that reduction in plant size of tomatoes with aucuba mosaic and of potatoes with mild and severe mosaics is due more particularly to smaller leaves and internodes than to fewer leaves and internodes. With regard to factors affecting efficiency, it is well established that both metabolism and translocation are adversely affected in diseased plants (vide Section 1, Part 2). Clearly then virus diseases affect yield to a greater extent than truss formation by reason of their more pronounced effect on size and efficiency than on numbers of units of shoot growth.

The anomolous result for virus Y is accounted for by the fact that in the counts made upon plants affected with this virus a number of incipient trusses were omitted owing to their small size and the consequent inability of the operator to count/

count the numbers of buds. The effect of this virus, as was shown in Tables 10 and 14, was greatly to reduce numbers of flowers and it is believed that the effect was even more pronounced than recorded in the data on account of the suppression of flowering in the very early stages of truss formation. The apparent reduction in numbers of buds per truss, recorded only for this virus, is ascribed to the same cause, namely, the non-development of buds from their primordia.

The second line of discussion may be directed to a consideration of the differential effects of the various viruses on flower and fruit production after elimination of their effects on truss formation. The summarised data given in Table 14 show that, except in the case of virus Y which may be disregarded in view of the possibility of inaccurate counting, the number of buds per truss was unaffected by virus infection. The number of persistent flowers and the number of berries per truss, on the other hand, were considerably reduced by the mosaic viruses and were relatively unaffected by the leaf roll virus. The reduction caused by the mosaic group of diseases, moreover, was greatest for virus Y, and least for virus X. Fertility, in relation to the number of persistent flowers/

flowers, was unaffected or even slightly increased in the diseased plants. The effects of virus infection upon flower and fruit production, therefore, are confined to the failure of flowers to persist to maturity and are most marked in plants affected with mosaic diseases.

The causation of premature abscission of buds and flowers has been traced to three interdependent groups of factors which may be briefly described as genetical, physiological and environmental. DORSEY (1919) failed to trace any connection between pollen abortion, lack of pollination and abscission. He suggested that physiological factors uninfluenced by ovule and pollen development were primarily the cause of abscission. STOUT and CLARK (1924) and USPENSKY found that environmental influences caused differential flowering responses within individual varieties. BLEIER (1931) traced abnormalities in reduction division, degeneration of pollen mother cells and the falling of buds, flowers and fruits to a single primary cause which he described as a hereditary abnormality in metabolism. Later, the same author (1933) suggested that a specific substance was responsible for the disturbed metabolism and, in the light of KOSTOFF'S (1933)/

(1933) observations upon abnormalities in pollen formation and seed production in mosaic tobacco, he further suggested that the specific substance was similar in nature to a virus. The analogy, however, even though substantiated, cannot be accepted as an explanation of the cause of abnormality since there is good evidence that viruses are not causes in themselves but merely agents affecting physiological processes. It is, indeed, most probable that the abscission of flowers is brought about by variations in the physiological balance of the plant whereby the expression of genetical factors is enhanced or modified. ELLISON (1936) has concluded similarly and has suggested that sterility is determined by two groups of factors, one of which is inherent in the variety and expressed as meiotic irregularities, and the other physiological and expressed in the retarded development of floral parts. He suggested further that the physiological factors were determined by the sum total of environmental influences, for example, nutrition, temperature, amount of sunlight and length of day.

In the present material the influence of genetical factors determining flower development and fruit formation may be seen in the difference in persistence between the normal plants of President and/

and those of Majestic. For the causes of differences between normal and diseased plants the possibilities of physiological factors must be explored. From the literature upon the effect of virus diseases upon the physiology of the host plant, (q.v. Section 1, Part 2) it is at once apparent that one of the primary effects of mosaic diseases is to cause alteration in the carbohydrate/nitrogen relationships of the plant through a reduction in carbohydrate and an increase in nitrogen. In view of the close connection which has been established between this relationship and flower production it is not unreasonable to seek the cause of reduced persistence of flowers, in which is included the non-development of buds, in disturbed metabolism affecting the relative amounts of carbohydrate and nitrogen. The lower persistence values in mosaic infected plants would be ascribed, therefore, to the lower C/N ratio in these plants.

Unfortunately there are no comparative data available with regard to the effects on metabolism of the three mosaic diseases used in the present study. A correlation between degree of persistence and extent of alteration of the C/N ratio cannot be attempted, therefore. Nevertheless, the fact that leaf roll has relatively little affect on persistence lends/

lends support to the view expressed above, for it has been shown by CAMPBELL (1925), BARTON WRIGHT and McBAIN (1932, 1933) and COCKERHAM (1933) that in leaf roll plants as compared with normal plants the nitrogen content is affected only slightly, and in the direction of reduction, whilst carbohydrates are affected greatly and in the direction of increase. There is reason to believe, however, that the effective C/N ratio is not greatly enhanced in leaf roll plants on account of the relative immobility of the accumulated carbohydrate. Consequently, persistence of flowers is not greatly increased. In this connection it is significant that in the variety Majestic, in which leaf roll caused a reduction in yield amounting to 59%, persistence was slightly greater in the diseased than in the normal plants whilst in President, in which leaf roll reduced yield by 95%, persistence was lower in the diseased plants. These data are very suggestive that movement of carbohydrate in leaf roll plants was greater in Majestic than in President and that the effective C/N ratio was correspondingly affected in favour of flowering in Majestic and against flowering in President.

SUMMARY

1. The comparative effects of leaf roll upon the yields of six potato varieties and of mosaic diseases upon the yields of two potato varieties have been studied in a small scale statistical trial.

2. Leaf roll was found to reduce significantly the yields of each variety but the extent of reduction varied considerably between varieties.

3. In the two varieties in which viruses were compared yield was reduced to the greatest extent by the leaf roll virus, to less but still considerable extents by the Y virus and the A + X complex, and to a small and insignificant extent by the X virus. The extent of reduction was related to the disease rather than to the virus.

4. The effects of virus diseases upon reproduction have been followed in two potato varieties.

5. The reproductive capacity, as measured on a per plant basis, was found to be reduced in plants affected with each of the viruses investigated, the primary cause of reduction being traced to a diminished number of flower trusses.

6./

6. The differential effects of virus diseases upon yield and truss formation have been discussed.

7. Flower and fruit formation in plants affected with mosaic diseases were found to be further reduced through lack of persistence of flowers. Number of buds and fertility of persistent flowers were unaffected. Persistence was relatively unaffected in leaf roll plants.

8. The causes of lack of persistence have been examined and traced to disturbances in metabolism affecting the carbohydrate/nitrogen relationships.

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Figure 1.

Arrangement of Plots in Field.

E	B	F	D	C	A	G	H	L	J	M	K	Q	R	O	S	P	N	T	U	V	W
F	A	B	C	D	E	M	K	H	L	J	G	P	Q	N	R	O	S	U	T	W	V
A	E	D	F	B	C	L	M	G	K	H	J	O	P	R	N	S	Q	T	U	V	W
D	F	C	A	E	B	J	G	M	H	K	L	N	O	S	P	Q	R	V	W	T	U
B	C	A	E	F	D	K	L	J	M	G	H	S	N	Q	O	R	P	W	V	U	T
C	D	E	B	A	F	H	J	K	G	L	M	R	S	P	Q	N	O	V	W	T	U

A. Alness, control.

B. Alness, Y, eliminated.

C. Alness, LR, leaf roll.

D. Di Vernon, control.

E. Di Vernon, Y, eliminated.

F. Di Vernon, LR, leaf roll.

G. Great Scot, control.

H. Great Scot, Y, eliminated.

J. Great Scot, LR, leaf roll.

K. Majestic, control.

L. Majestic, Y, eliminated.

M. Majestic, LR, leaf roll.

N. A. Victory, control.

O. A. Victory, Y, severe mosaic.

P. A. Victory, LR, leaf roll.

Q. President, control.

R. President, Y, severe mosaic.

S. President, LR, leaf roll.

T. A. Victory, X, mild mosaic.

U. A. Victory, A+X, crinkle.

V. President, X, mild mosaic.

W. President, A+X, crinkle.

Each plot contained 10 tubers in each of 2 drills. The tubers were planted at intervals of 2 feet and the horizontal rows were separated by a path 4 feet wide. All tubers were planted on 23rd. April, 1936 and all plants were lifted on 1st. October, 1936.

APPENDIX 1.

Analysis of yield - Tables 2 - 4

APPENDIX

TABLE 2

Mean Yields of Plots in lbs. per Plant.

VARIETY	ALNESS		DI VERNON		
Plot	Healthy	Leaf Roll	Healthy	Leaf Roll	Total
1	2.3750	0.6560	3.1063	0.9663	7.0436
2	2.6000	0.5833	3.0278	1.5208	7.7319
3	2.0313	0.8125	2.7250	1.0581	6.6269
4	2.3938	0.6875	2.5547	1.2031	6.8391
5	2.5694	0.5833	2.8482	1.1875	7.1884
6	1.9750	0.7594	2.9563	1.0833	6.7730
Total	13.9445	4.0180	17.2183	6.9591	42.2029

Analysis of Variance

Variance due to	Degrees of Freedom	Sum of Squares	Mean Square	$\frac{1}{2}$ loge Mean Square	Z
Plots	5	0.2095	0.0419	0.7163	-
Condition	3	18.4539	6.1513	3.2109	2.4693
Error	14	0.6168	0.0441	0.7416	-
Total	22	19.2802	-	-	-

1% point for Z, $n_1 = 3$, $n_2 = 14$ is 1.1457. Condition has therefore a significant effect on yield.

S.E. of plot = 0.070 lbs. S.E. difference = 0.099 lbs. Differences $>$ 0.297 lbs or $>$ 16.88% per plant are fully significant.

APPENDIX

TABLE 3

Mean Yields of Plots in lbs. per Plant.

VARIETY	GREAT SCOT		MAJESTIC		
PLOT	Healthy	Leaf Roll	Healthy	Leaf Roll	Total
1	4.0125	2.2917	4.0375	1.6875	12.0292
2	4.0804	1.3750	3.6938	1.2938	10.4430
3	3.5313	2.4063	3.9000	1.6805	11.5181
4	4.3313	2.2188	4.2569	1.6500	12.4570
5	3.6063	2.0125	3.9375	1.6641	11.2204
6	3.2313	2.1563	3.3938	1.4375	10.2189
TOTAL	22.7931	12.4606	23.2195	9.4134	67.8866

Analysis of Variance

Variance due to	Degrees of Freedom	Sum of Squares	Mean Square	$\frac{1}{2}\log_e$ Mean Square	Z
PLOTS	5	0.9255	0.1851	0.3079	0.1163
CONDITION	3	24.9903	8.3301	2.2112	2.0196
ERROR	15	2.2013	0.1467	0.1916	-
TOTAL	23	28.1171	-	-	-

1% point for Z $n_1 = 3$, $n_2 = 15$ is 0.8448. Condition has therefore a significant effect on yield.

S.E. of Total = 0.9329 lbs. S.E. of plot = 0.1555 lbs.

S.E. difference = 0.2199 lbs. Differences $>$ 0.6597 lbs. or $>$23.32% are significant.

APPENDIX

TABLE 4

Mean Yields of Plots in lbs. per Plot

VARIETY	CONDITION	1	2	3	4	5	6	TOTAL
PRESIDENT	H	30.76	30.94	38.31	34.13	29.24	33.06	196.44
	LR	1.63	1.56	2.00	1.25	1.25	0.98	8.67
	X	25.42	30.78	35.63	34.06	32.88	32.03	190.80
	A+X	10.63	10.63	15.09	10.42	9.27	9.20	65.24
	Y	12.08	11.46	8.54	12.92	8.13	8.54	61.67
ARRAN VICTORY	H	41.38	39.61	46.19	40.94	44.50	40.25	252.87
	LR	18.06	13.00	15.19	18.81	16.75	20.13	101.94
	X	34.20	46.88	32.50	36.67	32.19	32.19	214.63
	A+X	21.18	26.69	22.06	20.90	23.31	22.83	136.97
	Y	23.19	22.50	25.00	24.92	24.38	20.31	140.30
TOTAL		218.53	234.05	240.51	235.02	221.90	219.52	1369.53

Analysis of Variance

Variance due to	Degrees of Freedom	Sum of Squares	Mean Square	$\frac{1}{2}\log_e$ Mean Square	Z
Plots	5	40.2631	8.053	1.0431	-
Condition	9	8507.6398	945.293	3.4257	1.8990
Error	45	953.4735	21.188	1.5267	-
Total	59	9501.3764	-	-	-

1% point for Z with $n_1=9$, $n_2=45$ is 0.52. Condition has, therefore, a significant effect on yield.

S.E. of total = 11.27 lbs. S.E. of plot = 1.88 lbs. S.E. of plant = 0.188 lbs. S.E. of difference = 0.266 lbs. Differences $>$ 0.798 lbs. or $>$ 34.98% are fully significant.

APPENDIX 2.

Analysis of numbers of flower trusses, flower buds, persistent flowers, and berries per plant.

Tables 6 - 9.

APPENDIX

TABLE 6

	PRESIDENT (TRUSSES PER PLANT)					MAJESTIC	
	H	X	A+X	Y	LR	H	LR
M	19.25	17.50	10.00	3.73	11.23	11.95	7.00
SE_M	1.96	2.48	0.99	0.43	1.05	0.98	1.09
SD	8.77	6.08	3.29	1.66	5.85	4.36	4.86
SE_σ	1.39	1.75	0.70	0.30	0.74	0.69	0.77
D	-	1.75	9.25	15.52	8.02	-	4.95
SE_D	-	3.16	2.20	2.01	2.22	-	1.46
D/E_D	-	0.55	4.21	7.74	3.61	-	3.39
$n_1 + n_2$	-	26	31	35	51	-	40
P	-	> 0.5	< 0.01	< 0.01	< 0.01	-	< 0.01

TABLE 7

	PRESIDENT (BUDS PER PLANT)					MAJESTIC	
	H	X	A+X	Y	LR	H	LR
M	254.63	213.50	127.00	41.33	137.94	109.75	64.50
SE_M	23.76	28.71	3.79	2.55	13.19	8.50	9.69
SD	103.60	70.34	12.58	17.62	73.45	38.01	43.32
SE_σ	16.81	20.31	2.68	3.22	9.33	6.01	6.85
D	-	41.13	127.63	213.30	116.69	-	45.25
SE_D	-	37.27	24.06	34.85	27.17	-	12.89
D/E_D	-	1.104	5.30	6.12	4.30	-	3.51
$n_1 + n_2$	-	25	30	34	50	-	40
P	-	> 0.2	< 0.01	< 0.01	< 0.01	-	< 0.01

APPENDIX

TABLE 8

	PRESIDENT (FLOWERS PER PLANT)					MAJESTIC	
	H	X	A+X	Y	L.R.	H	L.R.
M	177.74	104.00	39.09	10.40	90.23	54.90	36.70
S.E.M	18.70	16.19	5.62	1.92	9.35	5.42	5.80
S.D.	81.51	39.65	18.65	7.42	52.04	24.24	25.94
$S.E._{\sigma}$	13.32	11.45	3.98	1.36	6.61	3.83	4.10
D	-	73.74	138.65	167.34	87.51	-	18.20
$S.E._D$	-	78.22	61.75	59.44	66.11	-	7.94
D/E_D	-	0.94	2.24	2.82	1.32	-	2.30
n_1+n_2	-	25	30	34	50	-	40
P	-	>0.3	>0.02	<0.01	>0.1	-	>0.02

TABLE 9

	PRESIDENT (BERRIES PER PLANT)					MAJESTIC	
	H	X	A+X	Y	L.R.	H	L.R.
M	15.63	18.00	3.36	1.40	8.61	7.85	4.90
S.E.M	3.17	5.50	0.88	0.62	1.46	1.32	1.12
S.D.	13.83	13.48	2.93	2.42	8.13	5.89	5.00
$S.E._{\sigma}$	2.24	3.89	0.63	0.44	1.03	0.93	0.79
D	-	2.37	12.27	14.23	7.02	-	2.95
$S.E._D$	-	6.35	3.29	3.23	3.49	-	1.73
D/E_D	-	0.37	3.73	4.40	2.10	-	1.71
n_1+n_2	-	25	30	34	50	-	40
P	-	>0.7	<0.01	<0.01	>0.02	-	>0.05

APPENDIX 3.

Analysis of numbers of flower buds, persistent flowers and berries per truss. Tables 11 - 13.

APPENDIX

TABLE 11.

	PRESIDENT (BUDS PER TRUSS)						MAJESTIC	
	H	X	A+X	A+X+?	Y	L.R.	H	L.R.
M	12.33	12.18	12.70	12.70	11.09	12.45	9.22	9.23
$S.E._M$	0.16	0.30	0.36	0.27	0.30	0.15	0.16	0.25
S.D.	3.13	3.12	3.79	3.20	2.23	2.87	2.51	2.86
$S.E._{\sigma}$	0.14	0.21	0.26	0.19	0.21	0.11	0.11	0.17
D	-	0.15	0.37	0.37	1.24	0.12	-	0.02
SE_D	-	0.34	0.40	0.31	0.34	0.22	-	0.20
D/E_D	-	0.44	0.93	1.18	3.67	0.54	-	0.08
n_1+n_2	-	491	494	527	441	731	-	371
P	-	>0.6	>0.3	>0.2	<0.01	>0.5	-	> 0.9

TABLE 12.

	PRESIDENT (FLOWERS PER TRUSS)						MAJESTIC	
	H	X	A+X	A+X+?	Y	L.R.	H	L.R.
M	9.15	7.30	3.91	2.57	2.74	8.08	4.55	5.34
S.E.M	0.23	0.36	0.41	0.27	0.36	0.23	0.23	0.30
S.D.	4.41	3.74	4.34	3.16	2.69	4.34	3.48	3.64
$S.E._{\sigma}$	0.16	0.26	0.29	0.19	0.25	0.17	0.16	0.22
D	-	1.86	5.24	6.58	6.42	1.07	-	0.79
$S.E._D$	-	0.43	0.47	0.35	0.42	0.33	-	0.26
D/E_D	-	4.30	11.09	18.77	15.12	3.26	-	3.011
n_1+n_2	-	474	479	511	426	715	-	370
P	-	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01

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TABLE 13.

	PRESIDENT (BERRIES PER TRUSS)						MAJESTIC	
	H	X	A + X	A+X+?	Y	L.R.	H	L.R.
M	0.80	1.12	0.34	0.02	0.36	0.78	0.66	0.71
SE_M	0.08	0.15	0.07	0.01	0.12	0.09	0.07	0.09
SD	1.52	1.52	0.70	0.14	0.75	1.59	1.10	1.06	1.06
SE_σ	0.06	0.11	0.05	0.01	0.07	0.06	0.05	0.07
D	-	0.32	0.47	0.78	0.44	0.03	-	0.05
SE_D	-	0.17	0.10	0.08	0.14	0.12	-	0.10
D/E_D	-	1.90	4.51	9.79	3.06	0.25	-	0.52
$n_1 + n_2$	-	474	479	511	424	713	-	369
P	-	>0.05	<0.01	<0.01	<0.01	>0.8	-	>0.6

SECTION III.

A Preliminary Survey of the Heritable Possibilities of Resistance to Virus Diseases of the Potato.

C O N T E N T S

INTRODUCTION.

Prior to the identification of viruses as the causative agents in potato degeneration the widely accepted belief in senility as the factor underlying this malady was sufficient in itself to limit the practical methods of control to the frequent transfer of vigorous seed from unaffected to affected areas, and the replacement of degenerated stocks by varieties newly raised from sexually produced seed. These are still the methods of control in use at the present day but, in the light of more precise information on the nature of the various pathogens causing degeneration, it is now possible to seek further and more complete control through the introduction of varieties resistant to or even immune from infection.

From a purely theoretical standpoint, potato varieties showing resistance to virus diseases may be classified into five types. These are,

1. Varieties which, under natural conditions, resist the act of infection. The type of resistance shown by such plants may be absolute or partial and may depend either upon anatomical features of the plant or upon factors which influence adversely the biotic relationship between plant and vector.

2/

2. Varieties in which the pathogen cannot exist after its introduction. This type of resistance is absolute and amounts to a natural immunity.

3. Varieties in which the virus, after infection has taken place, remains localised near the point of infection and does not become systemic.

4. Varieties in which the virus can exist in unchanged form without producing symptoms. Such varieties are of common occurence and are usually referred to as "symptomless carriers".

5. Varieties which although infected and showing symptoms of infection are not greatly affected in vigour and tuber production.

From the point of view of importance in practical agriculture the first type of resistance, that is resistance to infection, would appear to be the most valuable since it offers a measure of protection against most, if not all, of the commoner and more destructive viruses. It is not, unless absolute, preventative against ultimate degeneration, however, as varieties which show resistance to infection may prove to be very susceptible to specific viruses after infection has taken place. Plants of type 2, showing natural immunity to the pathogen, may offer a surer form of protection but in view of the wide differences in the natures of the four commonly occurring viruses/

viruses, namely, the X, A, Y and leaf roll types, it would seem that a plant, in order to be completely protected, would have to possess a fourfold immunity. Resistance due to localisation of the pathogen at the point of infection, type 3, may be considered to have affinities with resistance to the act of infection, type 1, since resistance is brought about by the failure of the pathogen to enter the tissues and become systemic. There is evidence to suggest that resistance of this type may be due to an extreme susceptibility of the plant and that localisation is brought about by the death of tissues in advance of the spreading pathogen. "Carrier" plants, whether symptomless, type 4, or symptom bearing, type 5, although valuable in themselves constitute a continual source of danger to more susceptible varieties. Their value is thus limited to conditions in which varieties, all "carriers" of the same virus, are grown in isolation from all susceptible varieties. Unfortunately, this restricted use of such varieties is not well recognised by present day agriculturists and "carrier" varieties are often grown in close proximity to susceptible varieties with the result that transmission/

transmission of virus is facilitated and stocks degenerate quickly. In view of the limitations placed upon their culture it is difficult to assess "carrier" varieties with respect to their peculiar qualities of resistance. With the imposition of suitable restrictions, however, and until the appearance of varieties possessing absolute immunity to infection and/or the pathogen, they have a definite economic value which merits their inclusion amongst the resistant types of practical utility.

Evidence suggesting that each of the aforementioned types of resistance are to be found in varying degrees has led to the supposition that genetical factors for resistance are available within the cultivated varieties of the potato. If this be the case then it is probable that the factors have become widely dispersed during the extensive hybridisation that has taken place in the search for varieties of improved yield and table quality.

The present investigation was undertaken with the object of examining this supposition of a genetical basis for resistance. It must be emphasised that the observations reported at this stage are hardly sufficient to admit of definite conclusions with/

with regard to either the nature of resistance or the method of its inheritance. It may be claimed, however, that sufficient evidence has been obtained to warrant a belief that the basis of resistance is inherent in the plant; that such resistance is dependent upon genetical factors which are transmitted from parent to offspring in an orderly manner; and that the number of factors involved, in the case of positive resistance, is high.

REVIEW of LITERATURE.

The historical literature of potato degeneration has been reviewed extensively by SALAMAN (1921, 1925a), ATANASOFF (1922b), DAVIDSON (1928) and SCARLETT (1933). It is at once apparent from these reviews that differences between potato varieties with regard to their susceptibility to "curl" or "Krauselkrankheit" were recognised long before the identification of the diseases with their causes. Even as early as 1779 an anonymous German writer, quoted by ATANASOFF loc. cit., observed that

> "This trouble appeared first only on the white Speiselkartoffeln; the Red and the large English Mastkartoffeln were free from it. In the year 1779 practically all white potatoes were destroyed, the Red and the English being also severely attacked whilst the Suppen- or so called Zuckerkartoffeln remained free from it".

In England YOUNG (1784) reported,

> "The Red-nosed kidney laid aside because it was sure to be curled. The Champion* generally preferred as it does not curl".

YOUNG repeated this statement in 1797 thus indicating that the variety Champion had retained its powers of/

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* Not the Champion raised by Nichol in 1863.

of resistance over a period of thirteen years at least. Similar observations upon varietal differences were recorded from time to time through the nineteenth century but with the possible exception of the Yam or Viehkartoffeln - a coarse potato chiefly used as animal food - no one variety appears to have been prominent in its capacity to withstand degeneration. Confusion must be guarded against, however, as it is quite probable that the observations recorded with regard to "curl" refer to both leaf-roll and mosaic diseases and that varieties which showed resistance to one later degenerated upon infection with the other. It is equally probable that many of the less susceptible varieties were "carriers" of mosaic viruses, a point to which attention has been drawn by DAVIDSON (1928) with regard to the old Champion. Evidence of the existence and recognition of "carriers" has, in fact, been provided by the observations of SIMON (1782), quoted by ATANASOFF (loc. cit.), that wherever the Viehkartoffel was planted in the neighbourhood of other varieties the latter degenerated. SIMON, indeed, dated the appearance of degeneration in Germany from the time of the introduction of the Viehkartoffel in 1770. STOCKMAR (1801) corroborated SIMON'S/

SIMON'S observations and carried out experiments to prove that infection proceeded from the Viehkartoffeln to other varieties planted contiguous with them. He concluded that the susceptible varieties were "hybridised" by the Viehkartoffeln and recommended that the latter should be grown apart from other varieties.

The connection between insects and degeneration was noted as early as 1802 by an anonymous contributor to the Edinburgh Farmer's Magazine. The same writer made the further observation that insects appeared to prefer one potato to another and that they would hardly touch a yam. (Yam is possibly a generic term used to indicate a coarse variety).

From these various citations it would appear that recognition of resistance types 1, 4 and 5 was made during the course of the 18th century. The literature covering the nineteenth century and the first twenty years of the present century is almost entirely concerned with the cause and control of degeneration and the subject of resistance does not appear again until the nature of the various pathogens had been established and the two classes of disease, namely leaf-roll and mosaic were differentiated. The references then become more specific in nature/

nature. COTTON (1921), reviewing the situation with regard to leaf curl and mosaic in Great Britain, expressed the opinion that although varieties were generally believed to vary markedly in susceptibility to virus diseases, the evidence at that time was not very conclusive. He put forward a list of commercial varieties which were often to be found in England infected with leaf curl and mosaic respectively but observed that whether this implied that the varieties were so infected because

(1) a large proportion of the stocks became infected in their early history,

(2) they had since been subjected to exceptional infection or

(3) that they were actually more susceptible,

could not be stated. He suggested, however, that it is probable that no variety is immune from either disease but that there is no doubt that the variety Great Scot is highly resistant.

The possibility of breeding resistant varieties appears to have been first mentioned by SALAMAN (1921) and ORTON (1921). SALAMAN in a series of subsidiary notes in later publications (1923, 1925[a], 1925[b], 1926) gives an indication of his own work in this direction. In 1923 he suggested/

suggested that as he had data to show that susceptibility to either mosaic or leaf-roll can be inherited separately and possibly in a Mendelian manner it is possible that resistance or immunity might follow along similar lines. Later (1925) he stated that although some wild species of potato are very highly resistant to leaf roll and mosaic the segregation observed in the progenies of crosses between these varieties and the domestic potato showed that resistance to virus diseases is closely linked to all the wild characters, viz. long stolons, scarcity of tubers, and extreme lateness. An observation linking colour and resistance to virus diseases was made by the same author (1926). Arising out of this relationship the suggestion was made that since those plants which possess the most colour are the most vigorous and most resistant to both leaf-roll and mosaic, then resistance may be closely allied to vigour and, like it, due to heterosis. These various observations remain, as yet, unsubstantiated.

MURPHY and McKAY (1925) pointed out that longevity of a variety is not due to immunity or resistance to infection but to a reaction of the plant to mosaic disease after infection has taken place. They/

They thus, by implication, recognised the difference between resistance to infection and resistance to the pathogen after infection.

The economic importance of "carrier" varieties was recognised by SALAMAN (1926) who pointed out that in the event of there being no other available means of combating virus diseases the solution of the problem might lie in growing only such plants as are "carriers". That this solution should be adopted only as a last resort is indicated by the statement in the same publication -

> "Our best hope must be that eventually resistant varieties will be raised which will replace those now in use."

The application of breeding methods directed towards the practical control of potato virus diseases has been in progress in America over a number of years and reports of the results obtained have been published by SCHULTZ and RALEIGH (1933), SCHULTZ, CLARK, BONDE, RALEIGH and STEVENSON (1934), STEVENSON and CLARK (1934), and by SCHULTZ, CLARK, RALEIGH, STEVENSON, BONDE and BEAUMONT (1937). These results indicate that a high degree of resistance to American mild mosaic (= A + X, European crinkle according to Murphy [1936]) and of immunity/

immunity to American latent mosaic (= X or X + X[B] MURPHY 1936, DYKSTRA 1936) has already been achieved. Owing to the empirical methods of breeding and testing employed in this work, knowledge upon the genetical mechanism underlying resistance to virus diseases has been little advanced. SCHULTZ and his co-workers (1934) state that their results provide evidence that some of the factors involved in the inheritance of resistance and susceptibility to mild mosaic are genetical in nature and that two or more factors, cumulative in effect, are necessary to interpret the data they have obtained from progeny tests in which transgressions for both resistance and susceptibility were found. Later (1937) they state that resistance to mild mosaic in field exposure is inherited as a dominant characteristic. No strictly genetical data are yet available, however.

In other species more favourable for investigation from the genetical aspect more progress has been made. The field bean (Phaseolus vulgaris), for example, has been the subject of a great deal of research into the nature of inheritance of resistance to virus diseases. Susceptibility to mosaic disease in this species was shown by McROSTIE (1921) to be dominant, or partially so, over resistance. A two factor/

factor control of these characteristics was postulated. PIERCE (1935) on the other hand, has provided evidence to show that resistance appears to be dominant to susceptibility in some varieties but that the inheritance of resistant characters is not entirely accounted for on a simple Mendelian basis. Reciprocal crosses between resistant and susceptible varieties showed slight differences in the proportions of resistant segregates, the differences being ascribed to cytoplasmic, but not necessarily inherited, influences. PARKER (1936) worked on very similar material to Pierce loc. cit. and came to the same general conclusion with regard to the inheritance of resistant characters. Contrary to PIERCE, however, he was able to trace a distinct maternal influence through his F_1, F_2 and F_3 progenies and concluded that his results showed evidence of cytoplasmic as well as Mendelian inheritance.

PORTER (1930) investigated the inheritance of resistance of cucumbers and found that susceptibility was dominant to resistance. No genetical ratios were established.

Amongst Solanaceous plants HOLMES (1934) has studied the inheritance of a differential reaction to a mosaic virus of tobacco in garden pepper (Capsicum/

(Capsicum frutescens), Nicotiana spp. and varieties of the egg plant. (Solanum melongena). His data show that localisation of the virus near the source of inoculation in the leaves of garden pepperwas controlled by a single dominant Mendelian factor, those plants bearing the recessive allelomorph responding to infection by the expression of systemic symptoms. Somewhat similar genetical factors were found to determine necrotic response to the virus infection of species hybrids of Nicotiana and varietal hybrids of Solanum melongena, although in these latter cases the inheritance was not as simple as that in Capsicum. HOLMES further established that the dominant factor was not linked with any other character and that the same factor controlled reaction to four different strains of the single virus used.

With regard to resistance to aphid attack, SEARLS (1935) has shown that in canning peas such resistance is an inherited character and is closely linked with yellow colouration of the foliage. No definite genetical ratios were established, however, although the data extend to the F5 generation.

The experimental work to be described in these/

these present studies has been based upon three interdependent lines of investigation, namely,

(1) a study of named varieties of potatoes in their reactions to the potato viruses X and Y;

(2) a genetical study of seedling material under conditions of artificial infection; and

(3) a study of named varieties and seedlings under conditions of natural infection.

It will be most convenient to examine the results obtained from each of these lines by collection of the data relative to each of the viruses concerned, namely virus X, virus Y and the leaf-roll virus.

EXPERIMENTAL OBSERVATIONS.

A. Virus X.

The X potato virus was first identified by SMITH (1931) although it has since been established that the diseases referred to as common mosaic, QUANJER (1923), tobacco ringspot, JOHNSON (1925) and SMITH (1929) and simple mosaic, MURPHY and McKAY (1932) are caused by this virus. The virus can be transmitted experimentally by all forms of sap inoculation and there is evidence that it is readily transmitted under natural conditions though no insect vector has yet been found. The present work has been confined to studies involving transmission by artificial means only.

Virus X is probably the most common virus found in the potato and apparently it occurs wherever the potato is grown (SMITH 1933). The reactions of potato varieties upon infection have been shown by SALAMAN and BAWDEN (1932) to be of two kinds; varieties may react either by showing symptoms of mild mosaic or by developing necrotic symptoms in the growing regions at the stem apex. This latter reaction has been described as top-necrosis or acro-necrosis by QUANJER (1931) and since the present investigation/

investigation has shown that all plants so affected are killed either in the year of infection or early in the year following infection it will be described as lethal top-necrosis.

1. Classification of named varieties.

The objective of this survey of named varieties with regard to their reaction to virus X was primarily their classification and later use as parental material for genetical study. A secondary object lay in the possibility that an examination of this nature might reveal factors for resistance resident in obscure varieties.

The methods used in testing the varieties were similar throughout and apply equally to the work on seedling varieties and to the controlled work on varietal reaction to virus Y. Prior to infection, each plant was examined for carried viruses by inter-varietal grafts and inter-specific inoculations. A large number of varieties were found to be infected with virus X and some with virus A. All were artificially infected, however, and the latter virus, although carried without symptom expression, was revealed by the formation of the virus complex A + X and the production of crinkle/

crinkle symptoms. A few varieties were found to be carrying virus B and virus D, BAWDEN (1934, 1936) which did not apparently affect the X reaction. The presence of these viruses are indicated in the table of results.

In view of the possibility that virus X may exist in several different strains, SALAMAN (1933), the source of virus was restricted to a single strain which had been preserved uncontaminated in the variety Arran Victory over a period of six years. It is believed, however, that the effect of strain is to be found only in intensity of reaction and not in type of reaction. All infections on to potatoes were made by grafting scions from infected Arran Victory. The plants were examined at frequent intervals, at least once each week, throughout the season. Those plants which responded to infection either as perfect or almost perfect carriers were subsequently tested for the presence of virus X by needle inoculation from them to Hyoscyamus niger which was used in the present work as an indicator of virus X. In the year subsequent to infection two tubers of each infected variety were grown in the field for verification/

verification, under natural conditions of growth, of the symptoms observed under greenhouse conditions. The classification is based on the observations made over the two year period and refers to at least two independent infections.

Classification of Varieties according to their reaction to Virus X.

Group 1: No reaction or very mild mosaic reaction to virus X. 11 varieties.
Aberdeen Favourite, Arran Scout (?), Celt (X), Di Vernon (D), Dunaverney, Field Marshal (X,B), Lochar (X), Mearns (X), Oran Beauty (X), Snowdrift, Up-to-date (X,B).

Group 2: Mosaic reaction to virus X. 81 varieties.
Abundance, Alannah, Ally, Alness, America, Argyll Favourite, Arran Banner, Arran Cairn, Arran Chief (X), Arran Comrade, Arran Consul, Arran Pilot, Arran Victory, Asset (X), Avondale, Baron, Beauty of Bute (X), British Queen, Champion, Chance, Claymore, Clovullin (X), Conquest, Cumnock, Doon, Pearl, Doon Star, Duke of Perth(X), Duke of York (X,B), Dunbar Cavalier, Dunnotar Castle, Early-field, Early Pink Champion (X), Early Rose/

Rose (X), Early Templar, Early Wonder (X), East Neuk, Eclipse, Edzell Blue (X), Evergood (X), Flourball, Gladstone, Glasgow Favourite (X), Gigantic, Glenalmond (X), Glencoe (X), Great Scot, Herald, Immune Ashleaf, Isla Star, Isle, John Bull (X), Jubel (X), Katahdin, Kerr's Pink (X), Kia Ora (X), King George V (X), Macbeth's Castle (X), Majestic, May Queen, Mein's Early Round (X), New Aberdonian (X), Nithsdale, Norna (X), Pepo, Perth Favourite, President, Puritan (X), Shamrock, Sharpe's Victor, Shetland, Spion Kop, St. Malo (X) Summit (X), Tinwald Perfection (X), Warba, Wild Rose, Witchhill (X), Wonderful (X), 70(13), 248(a)32 (X), 967c(38).

Group 3: Lethal top-necrotic reaction to virus X. 28 varieties:

Arran Crest, Arran Rose(?), Benalt, Benest, Cardinal, Crusader, Dean, Devanha, Dominion, Dunbar Yeoman, Epicure, Fiftyfold, Herd Laddie, Isis, Kepplestone Kidney, King Edward VII, Liddesdale Lads, Lymm Gray, Main's Surprise, Manxman, MaudMeg, Mighty Atom, Ninetyfold (?), Sharpe's Express, Thorn/

Thorn 2, Waverley, White City, Uncle Gideon's Quick Lunch.

(N.B. The brackets after certain varieties indicate the virus or viruses found in the stocks prior to the test infections)

In all, 162 named varieties have been tested and it will be seen from the classified list above that of these 120 were assignable to one of three major groups in respect of reaction to virus X. Group 1 contains 11 varieties which reacted to infection either as symptomless carriers, or with the production of very mild mosaic symptoms. Six of the varieties in this group were found to be already affected with virus X, one variety with Virus D, and another variety was doubtfully free from virus infection. Upon testing the grafted plants by inoculation to Hyoscyamus, virus X was recovered from all 12 varieties and none was immune, therefore, to infection. A very large proportion of the varieties tested fell into Group 2 which contains all those varieties reacting to infection by the expression of definite mosaic symptoms. Although the mosaic varied in intensity from plant to plant, none of the diseases was outwith/

outwith the mild mosaic group and no distortion of foliage was observed. 81 varieties fell into this group of which 30 were already infected with virus X.

The varieties in Group 3 all reacted to infection by the production of top-necrosis and all failed to produce sprouts in the second year or produced sprouts which were rapidly killed. There were 28 varieties in this group of which one was carrying virus E and two were doubtful carriers of unidentified viruses. Outwith the classification are 12 varieties carrying virus A alone and 30 varieties infected and showing symptoms of infection with one or more of the viruses A, X, Y and leaf roll. None of these varieties belongs to Group 3, though the position of each in Groups 1 and 2 could not be determined.

In the absence of precise knowledge upon the spread of virus X in the field it is difficult to assess the three groups of varieties from the point of view of economic value. The varieties in Group 2, however, may be considered inferior to either those in Group 1 or those in Group 3 since they possess to a greater degree all the disadvantages of "carriers" attached to the varieties of

Group/

Group 1 and they lack the advantages of the varieties in Group 3.

The position of the varieties in Group 3 is rather anomolous. Their reaction is one of complete susceptibility and infection results in death. In practice, however, extreme susceptibility of this type may prove a valuable characteristic since it is certain that at the beginning of each year, even though infection had been incurred previously, no X infected plants would appear above ground. In this respect the virus may be considered to be self-exterminating within the varieties of this group and all infection reaching them must necessarily arrive from sources external to the crop.

It is a matter of experience that the disease of top necrosis is rarely, if ever, seen in the field. The reason for this absence is at present obscure. Experimental evidence has accrued, however, to suggest that a virus causing necrotic reaction is localised at the point of entry into susceptible varieties, resistance type 3, and is thus prevented from becoming systemic. It is not proposed to discuss this latter point in the present instance as the essential fact is independent of the reason and is contained in the evidence that little or no transmission/

transmission of virus takes place into or within a variety which is necrotic to it. There is every indication, therefore, that extreme susceptibility may be a valuable asset in respect of virus control for not only is perpetuation of infector sources eliminated within the variety but also further infection from external sources is reduced to a minimum.

2. Genetical material.

The symptom reactions in 5 selfed and 11 hybrid progenies derived from parents in each of the three groups classified above has been obtained by the method of graft infection under greenhouse conditions. The parents used in this study were:

Group 1 (carriers); Up-to-date.

Group 2 (mosaic reactors); Great Scot, Kerr's Pink, Pepo, President, Shamrock, 70 (13).

Group 3 (necrotic reactors); Cardinal, Epicure, Kepplestone Kidney.

The variety Golden Wonder, a "carrier" of virus A and therefore unclassified, has also been used as a parent in one instance. Although the reaction of this variety to virus X cannot be determined with exactitude/

exactitude the fact that the complex A + X gives rise to anecrotic symptoms places the variety within either Group 1 or Group 2.

TABLE 1

Ref No.	Parentage	Parental Group No.	Segregation Nec.	Anec.	Total	Approx. Ratio
208	Kepplestone Kidney (B.S)	3	27	7	34	3 : 1
201	Up to date x Kepplestone Kidney	1 x 3	28	22	50	1 : 1
66	President x Kepplestone Kidney	2 x 3	50	50	100	1 : 1
48	Epicure x Pepo	3 x 2	10	12	22	1 : 1
50	Epicure x Shamrock	3 x 2	9	12	21	1 : 1
Total	Hybrid Progenies		97	96	193	1 : 1
26	Cardinal B.S	3	45	3	48	15 : 1
204	Cardinal x Kepplestone Kidney	3 x 3	16	0	16	16 : 0
68	Golden Wonder x Cardinal	1 or 2 x 3	74	12	86	54 :10

The/

The data relative to progenies derived from parents of the necrotic group are given in Table 1. It would appear from the ratios of necrotic : a-necrotic plants in these progenies that inheritance of the necrotic type of reaction follows Mendelian lines. Two distinct types of inheritance are indicated. The varieties Kepplestone Kidney and Epicure are apparently quite similar in constitution and the segregations in their F_1 progenies are suggestive of a single factor inheritance in which the factor controlling necrotic reaction is dominant. Although the data as expressed do not indicate the fact, plants bearing the recessive allelomorph of the necrotic factor may be either symptomless carriers or react to infection with the expression of mosaic symptoms.

The progenies relative to Cardinal differ from those above and the various ratios obtained are indicative of a multiple factor inheritance in which the factors controlling necrotic reaction are dominant though probably capable of modification.

TABLE/

TABLE 2.

Ref. No.	PARENTAGE	Group Number	Group 2			Group 1		Total	Group 2 : Group 1
			MM+	MM	MM-	TMM	None		
58	Pepo B.S.	2	2 2.7	35* 47.5	17 23.0	5 6.7	15 20.1	74 100	54 : 30 73.2 : 26.8
41	Up to Date x Pepo	1 x 2	- -	10* 14.5	26 37.6	13 18.9	20* 29.0	69 100	36 : 33 52.1 : 47.9
188	Dunbar Cavalier x Pepo	2 x 2	3* 8.6	19* 54.3	9 25.7	2 5.7	2 5.7	35 100	31 : 4 88.6 : 11.4
14	President x Pepo	2 x 2	- -	10* 41.7	7* 29.2	1 4.2	6 24.9	24 100	17 : 7 70.9 : 29.1
34	President B.S.	2	-	11 25.6	22* 51.2	5 11.6	5 11.6	43 100	33 : 10 76.8 : 23.2
207	70 (13) B.S.	2	8 11.8	24* 35.3	24 35.3	6 8.8	6 8.8	68 100	56 : 12 82.4 : 17.6
102	Great Scot x 70 (13)	2 x 2	4 4.8	44* 53.0	25* 30.2	6 7.2	4 4.8	83 100	73 : 10 88.0 : 12.0
198	Kerr's Pink x 70 (13)	2 x 2	7 9.5	41* 55.4	17* 23.0	6 8.1	3 4.0	74 100	65 : 9 87.9 : 12.1

* Parental type.

Progenies derived from parents in the anecrotic groups are detailed in Table 2. Considerable difficulties are met with in classifying symptoms within these groups and no strict limits between symptom classes can be imposed. There are certainly quite definite and readily observable differences between the MM+ ("severe" mild mosaic) type of reaction and the symptomless carrier type but the intermediate types merge gradually over the whole symptom scale. For purposes of analysis, however, it has been possible to subdivide Groups 1 and 2 into five arbitrary classes according to the severity of symptoms produced. These classes are indicated in the table by the symbols MM+, MM, MM-, TMM and no-symptoms in decreasing order of severity. It is proposed to use these symbols in discussing the data.

The most striking feature of the data in Table 2 is the evidence provided of transgressive inheritance of mosaic reaction in the selfed progenies of Pepo, President and 70 (13). This is seen with even greater clarity in the curves of Figure 1. In each progeny the modal type of reaction is that of the parent and trangression takes place in both directions/

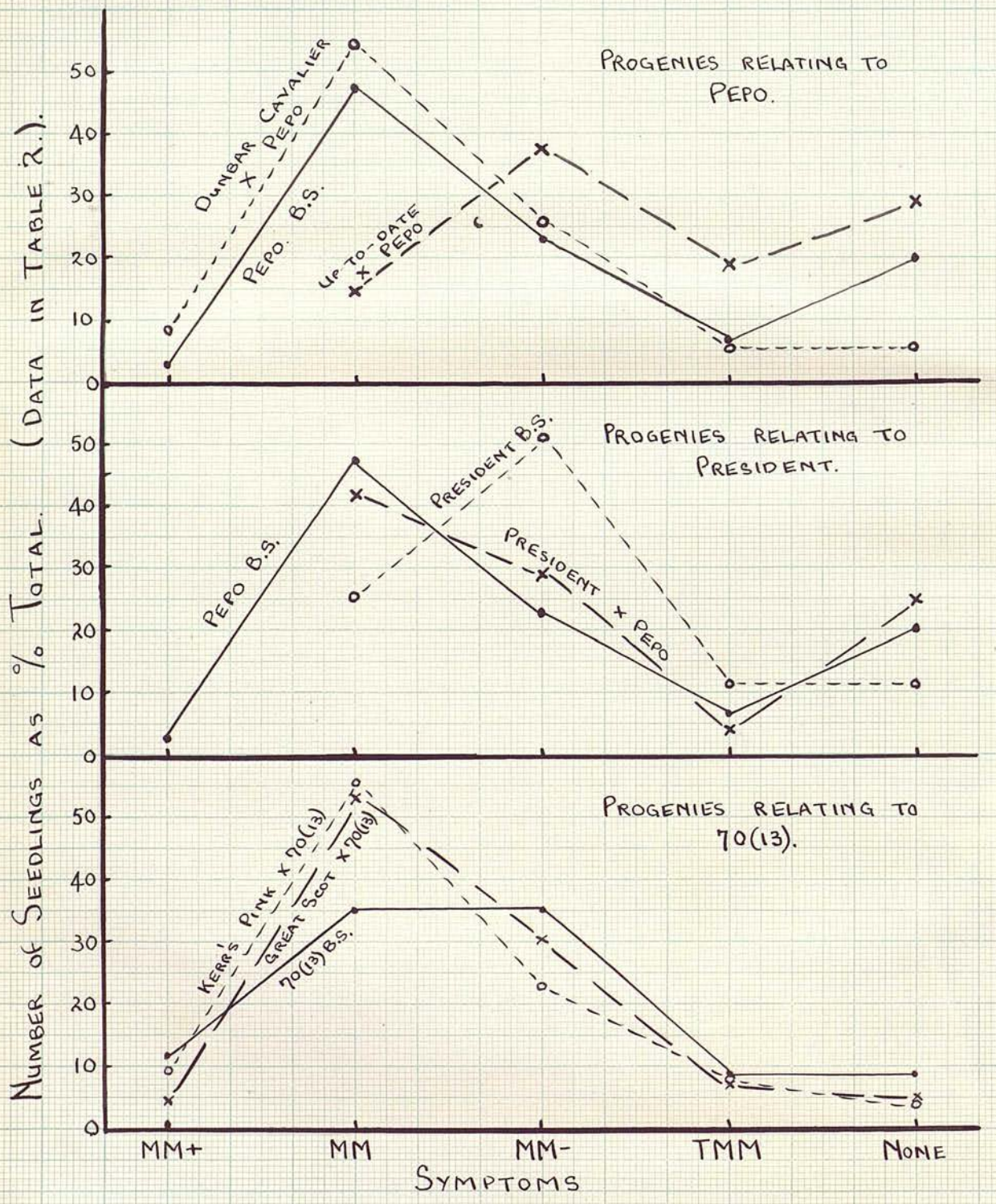

FIGURE 1. CURVES ILLUSTRATING TRANSGRESSION IN PROGENIES DERIVED FROM ANECROTIC PARENTS.

directions but not necessarily to equal extents. Thus in progeny 58, Pepo B.S.*, the prevailing type is MM and transgression is most marked in the direction of less intense symptoms. A similar tendency is evident in progeny 207, 70(13) B.S., but in this latter case there is a slightly greater proportion of the more severe types of mosaic and a lower proportion of the least severe. In progeny 34, President B.S., the modal type is MM- and the amount of transgression is approximately equal in both directions.

If now the various hybrid progenies are considered it will be seen that in progeny 31, Up-to-date x Pepo, the introduction of Group 1 characters by Up-to-date causes a transfer of the mode, as compared with that of progeny 58 derived from Pepo selfed, in the direction of less intense symptoms. The proportions of plants showing few or no symptoms are considerably increased. In progeny 188, on the other hand, an opposite effect resulting in an increased proportion of the most severe types of reaction and an increase in the modal types can be traced to the introduction of severe mosaic characters/

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* B.S. indicates that the flowers are protected from cross pollination.

characters from Dunbar Cavalier.

Progeny 14 derived from President x Pepo shows the influence of both parents by segregation of seedlings in the MM and MM- classes in proportions intermediate between those of the two parents and also by a slightly greater proportion of the no-symptom reaction than in either of the selfed progenies 34 or 58.

Progenies 102 and 198 were both derived from crosses between parents reacting with MM- symptoms and a common male parent, 70(13), which reacts with MM symptoms. The greater proportions of MM types and the lower proportions of MM+ and no-symptom types in the hybrid progenies as compared with the selfed progeny 207 may thus be taken to indicate that hereditary tendencies towards less intense symptoms shown by Great Scot and Kerr's Pink are opposed by greater tendencies towards more severe reactions in 70(13).

These various data are interpreted to show primarily that the behaviour of a progeny in its reactions to virus X is determined by the constitution of each of the parents and, therefore, that reaction is controlled by heritable factors.

The/

The wide range of symptoms in all progenies and the non-linear segregation of the no-symptom class in most of the progenies leads to the conclusion that a number of genetical factors are concerned. Furthermore, the small proportions of seedlings with severe symptoms is evidence of the presence of factors controlling the intensity of symptoms, that is, factors which may be considered in their effect to determine positive resistance to the pathological effect of the virus.

B. Virus Y.

Potato virus Y was identified and described by SMITH (1931) although many of its characteristic symptoms had been described previously under the term of streak, ORTON (1920), leaf drop streak, MURPHY (1921) and acropetal necrosis, QUANJER (1931), whilst ATANASOFF (1922[a]) and 1922[b]) considered the virus of stipple-streak to be the chief cause of potato degeneration and therefore traceable throughout the literature upon this subject. SMITH (1933) considers the virus to be one of the commonest and most destructive of potato viruses in England. The same author also gives a full description of the symptoms/

symptoms following infection in two groups of varieties, one group, containing the largest number of varieties, reacting to infection with the expression of "leaf-drop streak" and the other with symptoms of a mild mosaic mottling. Although the symptoms described by Smith are typical of a large number of varieties, a wide range of symptoms between the extremes of leaf-drop streak and almost symptomless carriers has been found. An arbitrary classification of the varieties according to their reaction to Virus Y has been based on two criteria, namely effect on vigour and presence or absence of necrosis. The details of classification are described below.

1. Classification of varieties according to reaction.

Potato varieties have been found to fall roughly into two groups according to the total effect of the virus on the plant, that is, in respect of reduction in plant size and vigour. Within each of these groups the primary symptoms following infection by grafting may be shown in one of two forms, with or without necrosis, and the groups have been subdivided according to the presence or absence of necrotic symptoms. The classification is therefore:

Group 1: Varieties upon which infection in its secondary stages is manifested by symptoms restricted to a slight puckering of the leaf surface which may or may not be accompanied/

accompanied by a slight chlorosis or mottle either of veinbanding or simple type. Plant vigour is not affected to any great extent.

Class (a) No necrosis in primary stages of infection. 9 varieties.
Arran Crest, Arran Rose (?), Benest, Catriona (A), Di Vernon (D), Doon Pearl, Herald, Scot (A), 70(13).

Class (b) Slight, often localised, necrotic symptoms in the primary stages of infection. 5 varieties.
Abundance, Earlyfield, Kerr's Pink (X), Mighty Atom, Nithsdale.

Group 2: Varieties upon which infection is followed by the secondary symptoms of severe puckering and reduction of the leaves together with chlorotic symptoms of various degrees of intensity. The typical symptom picture is that of severe mosaic with considerable reduction in vigour.

Class (a) No necrosis in primary stages of infection. 23 varieties.
Argyll/

Argyll Favourite, Arran Comrade, Arran Pilot, Arran Victory, Cardinal, Champion, Clovullin (X), Dominion, Dunnottar Castle, Early Templar, Gigantic, Herd Laddie, John Bull (X), Lochar (X), May Queen, Mein's Early Round (X), Norna (X), Pathfinder, Puritan (X), Uncle Gideon's Quick Lunch (A).

Class (b) Slight, often localised, necrotic symptoms in the primary stages of infection. 24 varieties.
Aberdeen Favourite, Arran Banner, Arran Cairn, Arran Chief (X), Claymore, Conquest, Cumnock, Duke of Perth (X), Dunaverney, Early Rose (X), Entente Cordiale, Fiftyfold, Flourball, Great Scot, Golden Wonder (A), Kia Ora (X), Lymm Gray, Macbeth's Castle (X), Shamrock, Sharpe's Express, Sharpe's Victor, Witchhill (X), Wild Rose, 967c(38).

Class (c) Severe necrotic lesions in primary stages of infection. Typical leaf-drop streak. 67 varieties.
Alannah/

Alannah, Ally, Alness, America, Arran Consul, Arran Scout, Asset (X), Avondale, Baron, Beauty of Bute (X), Benalt, British Queen, Buchan Beauty (A), Celt (X), Chance, Crusader, Dean, Devanha, Doon Star, Duke of York (B,X), Dunbar Cavalier, Dunbar Yeoman, Early Pink Champion (X), Early Wonder (X), East Neuk, Eclipse, Edzell Blue, Epicure, Evergood (X), Field Marshall (B,X), Gladstone, Glasgow Favourite (X), Glenamond (X), Glencoe (X), Glen Ericht (X), Immune Ashleaf Isis, Isla Star, Isle, Jubel (X), Katahdin, Kepplestone Kidney, King Edward VII, King George V (X), Liddesdale Lads, Main's Surprise, Majestic, Manxman, Maud Meg, Mearns (X), New Aberdonian (X), Ninetyfold (?) Oran Beauty (X), Pepo, Perth Favourite, President, Spion Kop, St. Malo (X), Summit (X), Up-to-Date (B,X), Warba, Waverley, White City, Windsor Castle (A), Wonderful (X), Yam (A), 248(a)32(X).

Judged from the standpoint of their powers of resistance to the pathogen after infection has taken place only those varieties in Group 1 of the/

the above classification can be considered of value to agriculture. All of the varieties in this group express symptoms, however, and must be placed in the fifth class of resistance shown on page 148. They are, moreover, all subject to the disadvantages of "carrier" varieties.

2. Genetical material.

The material available for a genetical study of the inheritance of the reaction to infection with virus Y has been limited to five small progenies derived from four parent varieties. The results of infection within each of three selfed and two hybrid progenies are given in Table 3 in which will be found the parental types and the proportions of segregates falling into each of the various classes of reaction established for the named varieties.

TABLE/

TABLE 3.

Ref. No.	PARENTAGE		Group 1		Group 2			
	Varieties	Groups	a	b	a	b	c	Total
207	70(13) B.S.	1(a)	30*	15	6	4	8	63
61	Chance B.S.	2(c)	2	1	2	3	6*	14
58	Pepo B.S.	2(c)	4	6	3	6	15*	34
192	Di Vernon x Pepo	1(a)x2(c)	15*	6	23	11	9*	64
197	Chance x 70(13)	2(c)x1(a)	3*	2	10	2	2*	19

* signifies parental type.

It will be seen from the table that seedlings of all five classes of reaction were found in each selfed progeny but that the predominating class in each was that of the parent type. In the two hybrid progenies, each of which were derived from crosses between parents in Group 1 (a) and Group 2 (c), and may be considered as reciprocals of each other in this respect, the Group 2 type of reaction predominated but it is of interest to note that the (a), anecrotic, reaction was found in greater proportion than the (b) and (c), necrotic, reactions even though these latter predominated/

predominated in the selfed progenies of the Group 2 (c) parents.

These data, though meagre, are at least indicative of the fact that progeny reaction is influenced greatly by parental type. They are too fragmentary, however, to justify even tentative conclusions as to the mode of inheritance involved.

3. Field Investigations.

a. Methods.

As the general plan of the investigations conducted in the field were identical for each of the two viruses studied, namely the Y virus and the leaf-roll virus, the following discussion of the methods used will apply to both. One of the essential conditions sought in the design of the trials was that of maximum uniformity compatible with maximum chances of infection and a minimum number of infector sources. It is believed that the arrangement shown in Figure 2 supplies these conditions. In this diagram infector plants are indicated by X and plants under trial by O.

Figure/

FIGURE 2.

	1 2 3 4 5 6 7 8 9, etc. DRILLS.
1	O O X O O O O X O O O O X O O O O X O O
2	O O O O X O O O O X O O O O X O O O O X
3	O X O O O O X O O O O X O O O O X O O O
4	O O O X O O O O X O O O O X O O O O X O
5	X O O O O X O O O O X O O O O X O O O O
6	O O X O O O O X O O O O X O O O O X O O
7	O O O O X O O O O X O O O O X O O O O X
8	O X O O O O X O O O O X O O O O X O O O
9	O O O X O O O O X O O O O X O O O O X O
10	X O O O O X O O O O X O O O O X O O O O

Under this arrangement the plots were limited in length of drill to 20 feet, sufficient to plant 10 tubers at intervals of 2 feet, the plot breadth being unrestricted except by the amount of space available in this direction. It will be seen by inspection that each infector plant is four plants removed, both in the drill and across the drills, from the nearest of its kind and that each plant/

plant under test is adjacent, either in the drill or across the drill, to one infector plant and adjacent diagonally to a second. Thus each plant under trial is situated similarly with respect to infector plants and is open to direct infection from two sources. The possibility of some plants showing extreme susceptibility and others extreme resistance owing to differential relationships with infector sources are consequently reduced to a minimum and differences between plants in their capacity to withstand infection may be considered as a measure of their resistance to infection and/or to the pathogen. It is not possible to examine every plant for its reaction to the virus by the method of artificial infection and, therefore, the field behaviour gives no direct information as to the type of resistance which may be shown. Since those plants which are observed to be infected in the field are by this fact proved to be susceptible to both infection and the pathogen, it is proposed to examine for type of resistance only those plants which withstand infection under field conditions over a period of at least three years.

The seedlings in the trials are inspected closely for symptoms of infection at each of four stages/

stages of growth. The first inspection is made in early July, prior to flowering, when late infection, unobserved in the previous year, is made evident. The second and third inspections are made during the course of the summer and the final inspection as late as possible, towards the end of September. At each inspection notes are made of the presence or absence of symptoms, the type and extent of symptoms when present, and of the major botanical characteristics of the plant if these are not already available. Notes on the distribution of aphides are taken independently and will be discussed later.

b. Experimental Observations.

The data relative to the spread of the Y virus through the seedlings of 10 progenies derived from seven parental varieties by self-fertilisation and hybridisation are presented in Table 4.

TABLE/

TABLE 4.

Ref. No.	PARENTAGE	% of Plants infected				TOTAL
		8/8/35	23/8/35	15/9/35	3/7/36	
Z4	Epicure x Pepo	-	-	61.5	94.9	39
41	Up-to-Date x Pepo	15.4	44.9	80.8	93.6	78
14,36	President x Pepo	25.9	51.8	87.0	88.9	54
35	President x Majestic	58.2	69.1	76.4	81.8	55
13,Z9	Arran Victory x Pepo	5.7	40.3	64.7	81.3	283
19,39	Majestic B.S.	-	-	76.7	-	60
32,34	President B.S.	25.7	37.1	60.0	71.4	35
12	Pepo B.S.	10.0	50.0	60.0	-	10
S(a)	Shamrock B.S.	-	-	42.3	-	26
50.Z5	Epicure x Shamrock	-	-	27.6	-	58

The significant features of these data are to be found in the large proportion of plants receiving infection after exposure during one season and in the differences in total infection between the/

the two progenies of Shamrock parentage and the remainder. It would seem from this latter observation that whereas the seedlings derived from the varieties Epicure, Pepo, Up-to-Date, President, Arran Victory, and Majestic show little or no resistance to virus Y, Shamrock possesses resistant qualities which are transmitted to its offspring and receive expression in the F_1 generation. Since all the varieties used as parents, Shamrock included, belong to Group 2 of the general scheme of classification it would appear that this resistance is against infection rather than against the pathogen.

The few plants of susceptible parentage which have remained uninfected may have escaped infection by chance or, on the other hand, they may possess a form of resistance. This latter alternative received support from the data obtained from the leaf-roll investigation and will be considered further in this connection.

In 1936 all the material remaining observably uninfected at the end of 1935 was replanted together with three progenies in their first year of test. The initial inspection was made on July 3rd 1936 and, as indicated in Table 4, a further proportion of infection was found in those progenies which/

which were under trial in 1935. This has been ascribed to infection having taken place late in 1935 and having remained unobserved on account of maturity effects. At this first inspection no plant in the progenies undergoing their first year of trial showed symptoms of infection. The second inspection, on 10th August 1936, revealed that a very small proportion of plants, less than 1% of the number planted, had become infected in the course of the season whereas 16% of the total number of plants in the trials during 1935 had received infection by 8th August of that year. This difference between the two years can be accounted for entirely by differences in the rate of multiplication of aphides and will be referred to in this connection. A severe attack of blight, first noticed on 8th August 1936, precluded any further observations upon the spread of infection during the season and the results for 1936 are held over therefore until the seedlings are available for inspection in the current year.

C. Leaf Roll.

1. Field investigations.

The data, in so far as they are available/

available, for progenies submitted to conditions of infection with the leaf-roll virus are presented in Tables 5, 6 and 7. Four progenies have been subjected to trial in the field over two complete seasons, 1934 and 1935, and the results indicate considerable differences between them in respect of the amount of infection contracted during this period. Three of the progenies were derived from crosses in which Pepo was the male parent. Of these 81.7% of the seedlings with Abundance as the female parent contracted infection. The proportions of leaf roll plants in the progenies having Arran Victory and Epicure as the female parents were 46.1% and 45.0% respectively. The fourth progeny was of the parentage Epicure x Shamrock and, after two years' exposure, showed only 28.6% of the plants to be infected with leaf roll.

TABLE 5.

Ref. No.	PARENTAGE	No. of Plants	% Leaf roll	
			1934	1935
Z1	Abundance x Pepo	104	55.8	81.7
Z9	Arran Victory x Pepo	102	9.8	46.1
Z4	Epicure x Pepo	46	25.0	45.0
Z5	Epicure x Shamrock	70	12.9	28.6

It/

It will be seen from the comparative figures for 1934 and 1935, Table 5, that although the relative susceptibilities of the four progenies were indicated after one year's exposure to infection, 1934 data, the extent of infection increased after a second year of exposure and the results were more strictly comparable at the end of this period. The proportions of infected seedlings given in Table 6 must be examined with reserve, therefore, as they refer only to the results of a single year's trial. The figures given for 1935 are those for symptoms of infection seen prior to harvesting the seedlings in October of that year and those for 1936 refer only to plants which showed symptoms during the early stages of growth, thus indicating that infection had taken place late in the 1935 season. Further reference will be made to this question of late infection in a consideration of the problems of seasonal multiplication and spread of the aphid vectors.

TABLE/

TABLE 6.

Ref. No.	PARENTAGE	No. of Plants	% Leaf Roll 1935	% Leaf Roll 1936
41	Up-to-Date x Pepo	80	5.0	55.0
19 and 39	Majestic B.S.	59	10.2	35.6
14 and 36	President x Pepo	52	1.9	30.8
35	President x Majestic	55	-	27.3
32 and 34	President B.S.	53	1.9	26.4
13	Arran Victory x Pepo	199	3.0	28.5
50	Epicure x Shamrock	21	-	9.5
22 & S(a)	Shamrock B.S.	55	-	3.6

It is quite clear from the table that the greater part of leaf roll infection was contracted late in the season and was not expressed until the following year. It is also clear that progeny 41 contained a larger proportion of susceptible seedlings than any other progeny and that the seedlings derived from Shamrock were much more resistant than those of other parentage. Further evidence must be examined before conclusions can be drawn, however.

2/

2. Controlled infection.

In order to amplify the field observations and eliminate discrepancies due to possible unequal distribution of aphides in the field, a series of data have been obtained from material placed under conditions of controlled infection. For this purpose a supply of virus-free aphides, Myzus persicae, was obtained from Dr. Kenneth Smith of the Potato Virus Research Station, Cambridge, and subsequently cultured on leaf-roll bearing plants of Arran Victory enclosed in muslin covered cages. The aphides were allowed to feed and multiply on the diseased plants for 50 days and were than transferred to the sprouts of seedlings prepared by planting the tubers in shallow boxes so that the young sprouts were exposed just above soil level. At the time of test the sprouts of the different seedlings varied from ½ inch to 1½ inches in length. Six aphides were placed on each tuber and allowed to feed for ten days. At the end of this period the boxes were fumigated and the tubers planted in the field, well isolated from other potatoes. The percentage distribution of leaf roll in each of the seedling progenies infected in this manner is given in Table 7. For comparison the relative data for the same progenies subjected to natural field infection are also given.

TABLE/

TABLE 7.

Ref. No.	PARENTAGE	No. of Plants	% infection in					
			Sprouts & Field	Sprouts only	Field only	Total Sprouts	Total Field	Total
41	Up-to-Date x Pepo	77	39.0	36.4	13.0	75.4	49.4	88.4
19	Majestic B.S.	27	33.3	29.7	18.5	63.0	48.2	81.5
14 and 36	President x Pepo	52	21.2	46.2	7.7	67.4	28.9	75.1
35	President x Majestic	54	14.8	44.4	13.0	59.2	27.8	72.2
13	Arran Victory x Pepo	196	10.7	31.1	17.3	41.8	28.0	59.1
50	Epicure x Shamrock	21	9.5	52.4	-	61.9	9.5	61.9
22	Shamrock B.S.	13	-	7.7	7.7	7.7	7.7	14.4

It will be seen from the table that although the percentage of infection produced under the controlled conditions, i.e. by sprout infection, was much greater than that contracted in the field the differences/

differences between the progenies in their response to infection were equivalent under both sets of conditions. Thus progeny 41, derived from the cross between Up-to-Date and Pepo, showed the largest proportion of infected seedlings in both series of trials whilst progeny 19 was second in this respect. The proportions of infected plants in the two progenies 14 + 36 and 35, in which President was the female parent, Pepo and Majestic being the respective pollen parents, were almost equal within each trial and equivalent between the trials but showed a relatively larger increase in sprout infection over field infection than the more susceptible progenies 41 and 19. This increase was also observed in the case of progenies 13 and 50 being particularly noticeable in the latter which was derived from Epicure x Shamrock. Of the 13 seedlings raised from self-fertilised seed of Shamrock, 1 plant showed doubtful symptoms of leaf-roll in the field infection trial and 1 in the sprout infection trial.

TABLE/

TABLE 8

PARENTAGE	Leaf roll				Y virus	
	Field 1 year	Field 2 years	Sprouts	Total	Field 1 year	Total
Abundance x Pepo	55.8	81.7	-	-	-	-
Up-to-Date x Pepo	55.0	-	75.4	88.4	80.8	93.6
Epicure x Pepo	25.0	45.0	-	-	61.5	94.9
Majestic BS	35.6	-	63.0	81.5	76.7	-
President x Pepo	30.8	-	67.4	75.1	87.0	88.9
President x Majestic	27.3	-	59.2	72.2	76.4	81.8
President BS	26.4	-	-	-	60.0	71.4
Arran Victory x Pepo	9.8	46.1	-	-	71.0	90.0
Arran Victory x Pepo	28.5	-	41.8	59.1	61.6	77.2
Epicure x Shamrock	12.9	28.6	-	-	-	-
Epicure x Shamrock	9.5	-	61.9	61.9	27.6	-
Shamrock B.S.	3.6	-	7.7	3.6	42.3	-

The combined data upon infection through the agency of aphides have been brought together in Table 8. If these data are examined in the light of the/

the known facts obtained by field and greenhouse studies of the parents it becomes quite evident that resistance and susceptibility in their widest sense, are heritable characteristics, for the varieties Abundance, Up-to-Date, Pepo, Majestic and President are known to be very susceptible to infection in the field whilst Epicure and Arran Victory are fairly resistant and Shamrock is quite resistant. With regard to the Y virus, however, all the varieties have been shown to belong to the more susceptible groups of varieties in respect of their reactions to the pathogen and the proportion of infected plants in the progenies would appear to indicate that none of them, with the exception of Shamrock, possesses any high degree of resistance to infection. It would seem then that the lower proportions of leaf-roll infected seedlings in the progenies derived from Epicure and Arran Victory are due to the expression within the uninfected seedlings of characters determining resistance against the pathogen rather than against infection whilst in the Shamrock seedlings it is entirely possible that resistance of both types is expressed.

SUMMARY and CONCLUSIONS.

The results of this preliminary survey have given considerable support to the supposition that genetical factors for resistance to each of the viruses X, Y and leaf roll are present within the cultivated varieties of potato and it has been quite clearly established that the factors are many and are widely dispersed throughout the varieties at present in commercial use.

With regard to virus X, a study of the reaction of 162 named varieties and 947 seedlings has established the fact that at least one reaction to this virus, that of lethal top necrosis, is determined by the presence of one or more genetical factors which are inherited in Mendelian fashion. The further evidence of the transgressive inheritance of the mosaic reaction is suggestive that, in addition to factors determining necrotic reaction, there are also factors which determine a positive resistance against the expression of mosaic symptons.

A consideration of these results leads to the suggestion that two possibilities are open to the potato breeder with regard to the control of virus/

virus X. In the first place a practical measure of control may be found in the use, as parents, of varieties which are fully susceptible to the virus and respond to infection with a lethal top necrosis. Since this type of reaction is inherited in dominant fashion there should be little difficulty in using this character as a protective measure in the manner described for the varieties of Group 3 in the classification according to reaction to virus X.

Secondly, there is the possibility of aggregating the factors for positive resistance so that a high degree of resistance, amounting to virtual immunity, is built up. The discovery of an "immune" seedling by Schultz et al (1934) is very suggestive that such a possibility is not too remote. It is interesting to note in this connection that according to Müller (1930) resistance to blight, Phytophthora infestans, in the potato is controlled by the cumulative interaction of four allelomorphic genes, in two factor pairs, and that the degree of resistance is determined by the number and relative strength of the genes present in the genotype. A similar suggestion in relation to the inheritance of resistance to wart disease was made later by Black/

Black (1935) who postulated that three factors or groups of factors, each of which acts independently determine the degree of resistance to wart disease by their number and relative strength in the genotype. It is quite possible that a similar series of factors determine the resistance of potato varieties to virus X.

The data for virus Y have been derived from 128 named varieties, 194 seedlings which have been infected artificially and from 698 seedlings which have been subjected to infection under natural conditions. Although these data have given indication that reaction to virus Y is heritable and that it might be possible to secure partial control by breeding from varieties which are little affected by the virus, there is as yet little evidence of a high degree of positive resistance against the virus. It has already been shown in section 2 however that varieties showing similar symptoms may be differently affected in vigour. This evidence together with the results of genetical study showing that segregation of reaction types takes place in seedling progenies, provides some indication that factors controlling positive resistance may be present within the species. At present, however, the most likely method of control seems to be available in the differential response/

response of varieties with respect to their abilities to withstand the entry of the virus under conditions of natural infection. The results obtained from the field trials have indicated that resistance of this type is inherited and, therefore, of value in breeding.

The results with regard to leaf-roll have been obtained from field trials of 162 named varieties and 896 seedlings and from 440 seedlings subjected to infection under controlled conditions. These results are very similar to those for the Y virus and are even more strongly suggestive that control may be obtained most readily by the use of parent varieties which resist the entry of the virus. Again, however, indication has been given of a positive resistance against the pathogen and this may prove ultimately to be of considerable value.

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PLATE 1. Virus X on leaf of Arran Victory. Mild mosaic symptoms of MM type.

PLATE 2. Virus X on three seedlings of Pepo B.S. Left, mild mosaic symptoms of type MM-. Centre, no symptoms on "carrier" variety. Right, mild mosaic symptoms of type MM+.

PLATE 3. Virus X on Edgecote Purple. Early stages in lethal top necrosis.

PLATE 4. Virus Y on Shetland. Group 1; Class (a). Symptoms restricted to slight leaf puckering and slight veinal mosaic.

PLATE 5. Virus Y on Harbinger. Group 1; Class (b). Symptoms restricted to slight leaf puckering with veinal mosaic and slight necrosis. No marked dropping of leaves.

PLATE 6. Virus Y on Stirling Castle. Group 2; Class (a). Severe leaf puckering and severe mosaic typical of plants in Group 2. No necrosis.

PLATE 7. Virus Y on Thorn 1. Group 2; Class (b). Fairly severe mosaic symptoms with slight necrosis. No marked dropping of leaves.

PLATE 8. Virus Y on Duke of Kent. Group 2; Class (c). Severe and typical leaf-drop streak.

SECTION IV

A Preliminary Study of Aphis Populations and the Spread of Virus Diseases within Potato Crops.

C O N T E N T S

INTRODUCTION

The association of the spread of potato virus diseases with the distribution and multiplication of the aphides infesting the potato crop was probably first identified with certainty by SCHULTZ, FOLSOM, HILDEBRANDT and HAWKINS (1919). These authors observed that in their experimental plots at the Maine Agricultural Experiment Station aphides, which were noticeable on potato plants in the latter half of July 1918, had become very numerous about the middle of August and were more excessively abundant at the end of the month. In one experiment over this period they removed one tuber from each plant of their test crop, Green Mountain variety, on 15th August and a second on 26th August, whilst the remainder were harvested on 12th September. The tubers from each selection were planted in 1919 and were found to produce 6%, 14% and 50% of mosaic plants respectively. From this result they concluded that the late infection of the tubers was due to the late development of the chief cause of spread mosaic, namely, abundant dispersing aphides. Further observations by SCHULTZ and FOLSOM (1920, 1923, 1925) confirmed this early work and extended it/

it to cover other virus diseases of the potato. They found that the aphides Macrosiphum solanifolii Ash. (= M. gei Koch) and Myzus persicae Sulz. were the chief vectors concerned. It has since been established by ELZE (1927, 1931), SMITH (1929) and DAVIES (1932) that in Europe Macrosiphum gei is at most of problematical importance in the spread of virus diseases and that Myzus persicae is the species of greatest significance in this respect.

An observation of particular interest with regard to the dissemination of aphis-borne viruses was made by ELZE (1927) who suggested that the introduction of viruses into a healthy potato crop is related directly to the arrival of the first alate generation of aphides in the early summer. This suggestion has received considerable support in fact and principle from the ecological studies of DAVIES and his co-workers in Wales (1932a, 1932b, 1934, 1935a and 1935b). Briefly stated these studies have shown that Myzus persicae is the chief vector concerned in the spread of virus diseases; that initial infection of a healthy crop is dependent chiefly upon the early summer migration of infective aphides from cruciferous plants, which serve as winter hosts, to the potato; and that spread within/

within the crop is thereafter dependent upon the rate and extent of multiplication of the apterous generations. The factors governing migration of the alatae have received particular attention and it has been found that temperature, wind velocity and relative humidity of the atmosphere are all concerned, the optimum conditions obtaining when temperature exceeds 65°F, wind velocity is less than 5-6 m.p.h. and relative humidity is less than 75%. With regard to the seasonal variations in aphis populations, it was found that in North Wales the maximum infestation, in normal years, is to be expected in mid-July although the time is dependent to a large extent upon climatic factors.

Data relative to the aphid populations of potato crops in Scotland are very meagre and apart from general observations made in Aberdeenshire during the seasons 1931-1934 they have been collected from three limited surveys, each extending over a period of a few days only, made in July 1931, August-September 1934 and July 1936. The only published observations are those of SMITH (1933a and 1933b), who reported that in July 1931 Myzus persicae was found in small numbers on experimental plots at Corstorphine, Edinburgh, and that further inspections in Ayrshire and Aberdeenshire revealed a scarcity of these/

these aphides. In the early observations of 1931-1934, made by the writer whilst stationed at Huntly, Aberdeenshire, Macrosiphum gei was found in small numbers during July and August, but no large infestation was recorded at any time. Myzus persicae was readily found in small numbers during September but never reached the proportions of a large infestation, probably owing to the early frosts experienced in the district.

The present data have been collected with a twofold purpose in view, namely, to amplify and extend the scanty information already available for the distribution and multiplication of aphides under Scottish conditions and also to obtain more precise information upon the aphis populations within the particular environments in which the potato breeding trials of the Scottish Plant Breeding Station are carried out. The work has been directed chiefly towards a correlation of aphis populations and the apread of virus diseases within the crop since this aspect of the problem is of particular importance in the studies which are in progress upon the inheritance of susceptibility and resistance to virus diseases.

AREAS OF SURVEY

The observations made at the Plant Breeding Station, Corstorphine, Edinburgh, were restricted to the experimental potato plots in each of two fields, (see Appendix, Figures 1 and 2). Each field is approximately 200 feet above sea level but though they adjoin, each has a different exposure. Field A slopes slightly to the south and east and is sheltered slightly on the north by a low thorn hedge. Field B, on the other hand, slopes slightly to the south and west and is bordered on the east by a relatively high thorn hedge. In 1935 the plots were situated as shown in Figure 1 and the leaf roll plots in Field A were completely exposed whilst the Y virus plots in Field B were sheltered. In the following year, Figure 2, the plots in Field A were sheltered and those in Field B were relatively exposed.

A further centre at the Ainville sub-Station, Kirknewton, Midlothian, was examined in 1936. The environment here is quite different from that at Corstorphine as the field investigated lies 850 feet above sea level, is completely exposed towards the south and is situated in a relatively sparsely populated and non-arable area.

METHODS.

In 1935 the observations upon aphides were confined to a survey of species distribution and non-statistical estimates of size of population. Inspections were made at weekly intervals from 5th July to 4th October and at each inspection records were made of the relative frequency of the various species of aphides, their stages of development and their particular environment, whether on leaves or in flowers. The results of these observations appeared to merit more detailed investigation, particularly with regard to the seasonal increase in numbers of aphides and the influence of variety upon the size of aphis population. The estimates at each centre in 1936, therefore, were obtained by counting the numbers of aphides on 100 leaves taken at random through each of three experimental crops. This method of estimation has been shown by DAVIES (1934) to give a reliable index of the aphis population. The three experimental crops used in investigation were Alness, a second-early, free-flowering variety; seedling 967 (c) 38, a late main-crop with blight resistant leaves; and the miscellaneous collection of named varieties and seedlings brought together in the susceptibility trials.

EXPERIMENTAL OBSERVATIONS

The following general observations upon aphis species and their relative distribution have been made in the course of the survey. At each centre and at all times of the season Myzus persicae, SULZ. was the predominant species and constituted 80-90% of the total aphis population. The remaining 10-20% was made up chiefly of Macrosiphum gei, KOCH., which was taken in all forms and at each inspection but never in large numbers. This species was most frequently observed to colonise the flowers and the records for 1936, since they refer only to aphides found on the leaves, are probably underestimates of the total population of M. gei. Occasional individuals of Myzus pseudosolani, THEOB. were observed and, in addition, a few aphides of unidentified species. The numbers of aphides given in the Tables include all species but they may be taken primarily as an index of the predominating species, Myzus persicae.

Of other insects observed with regularity upon potatoes, a species of Thrips was common in flowers and a capsid, Lygus sp., together with two species of Collembola were most common on the leaves. None of these has been associated with the spread of potato/

potato viruses, however, and records of their distribution and numbers were not made.

At the earlier inspections of each year aphides were usually found solitary or in very small numbers upon the leaves and were most frequently in the nymph or early adult stages of development. When increase in numbers became marked nymphs and adults were found together in colonies and, in many instances, both alate and apterous adults were observed in the act of depositing young. Winged forms were rarely found in the early summer but became more common towards the end of the season.

These latter observations may be taken to indicate, in the light of DAVIES' (1934) evidence, that migration in early summer had ceased before the inspections began in July and that the increase in aphis population during the summer was due entirely to multiplication within the crop.

Aphis Populations, 1935.

It has already been stated that the estimates of the aphis populations in 1935 were based on non-statistical observations. In Field A the estimates were obtained from the leaf roll trial plots and at the first inspection on 5th July occasional individuals of Myzus persicae and Macrosiphum gei were/

were found on the leaves and flowers respectively. No change in numbers or distribution was observed until 16th August when a few alatae of both species were seen and the numbers of apterous forms, particularly of M. persicae appeared to be increasing. The increase in this species was very marked one week later, 23rd August, and maximum infestation was attained on 29th August. After this date the numbers diminished slightly and progressively until the observations were terminated by severe frosts which occurred on 7th October. At no time was there indication of intensive attacks by predators or parasites.

In Field B, which contained the Y virus trial plots, the numbers of aphides were always slightly greater than in Field A. The increase in numbers, moreover, became perceptible on 2nd August, two weeks earlier than in Field A, and the maximum infestation was reached on 23rd August, as compared with 29th August in Field A. These differences point to a more favourable environment for aphides in Field B and, since the experimental material was similar in both fields, it would seem that the relative situations of the plots was the determining factor.

Aphis/

Aphis populations, 1936. Corstorphine.

The differences observed in 1935 between the aphis populations of the plots in Field A and those in Field B were not repeated in 1936. As the situations of the experimental plots were more nearly equal, the plots in Field A being more sheltered than in 1935 whilst those in Field B were slightly more exposed, there is further evidence of the influence of local environment on the size of aphis populations. The data given in Table 1 refer to Field A only since all three experimental crops were grown in this field.

TABLE 1

CRAIGS HOUSE, FIELD A.

DATE	No. of Aphides per 100 leaves			% infested leaves		
1936	ALNESS	MISC.	967(c)38	ALNESS	MISC.	967(c)38
July 25	19	-	-	7	-	-
Aug. 1	44	-	-	14	-	-
8	76	18	54	26	6	26
15	98	135	190	38	40	70
22	154	90	640	56	33	80
28	182	124	920	50	56	100
Sep. 8	-	434	1796	-	78	98
24	-	314	378	-	76	84

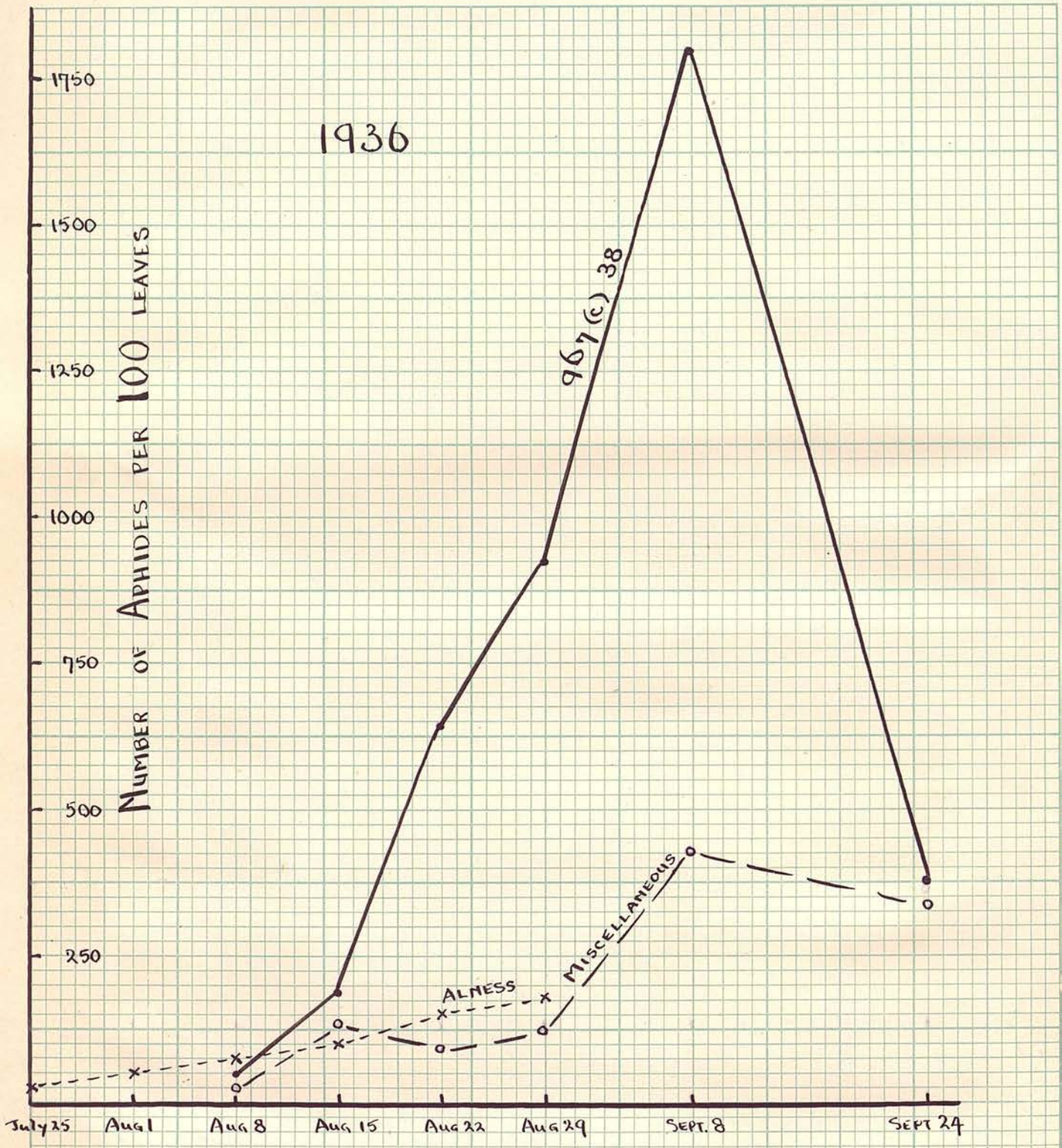

FIGURE 3. SEASONAL VARIATIONS IN THE APHIS POPULATIONS OF THREE POTATO CROPS AT CRAIGS HOUSE, CORSTORPHINE.

If the table is examined firstly with regard to the seasonal changes in numbers of aphides it will be seen that the size of the aphis population increased rapidly during August and reached maximum values on all three experimental crops during the early part of September. This is quite corroborative of the general trend of seasonal distribution during 1935 although there is indication that the maximum in 1936 occurred slightly later than in the previous year. From the aspect of spread of virus diseases a point of importance to be noted is that the proportion of infested leaves increased with increasing numbers of aphides, a fact which indicates that the increase in aphis population was not due entirely to multiplication in situ but also to movement of aphides from leaf to leaf and plant to plant during multiplication.

If the data are now examined to compare varieties, it is at once apparent that both the numbers of aphides and the numbers of infested leaves on the variety 967 (c) 38 exceeded considerably those on the variety Alness and on the miscellaneous seedlings. The variety 967 (c) 38 is a late maincrop with very large, blight resistant leaves affording excellent cover and hence, apparently, providing a most suitable environment for aphis/

aphis multiplication. Alness, on the other hand, is a second early variety which, in 1936, became fairly severely affected with blight during August. This latter factor alone undoubtedly affected the aphis population whilst the fact that the variety was maturing before maximum infestation occurred on later varieties may also be considered as a factor affecting numbers of aphides. The miscellaneous seedlings varied considerably with regard to maturity, size, shape, form, texture and blight resistance of the leaves. It was observed, however, that plants with an open habit of growth and with small coarse leaves tended to remain free from infestation in spite of the fact that their immediate neighbours harboured numerous aphides. These observations lead to the suggestion that varietal differences in susceptibility to virus infection under field conditions may be due, in part, to differences of maturity and, under certain conditions of blight resistance, but also to morphological differences affecting the ecological relationships between plant and insect vector.

Aphis populations, 1936. Ainville.

The seasonal increase in aphis population at the Ainville sub-Station during 1936 was very similar to that already examined for Corstorphine. The/

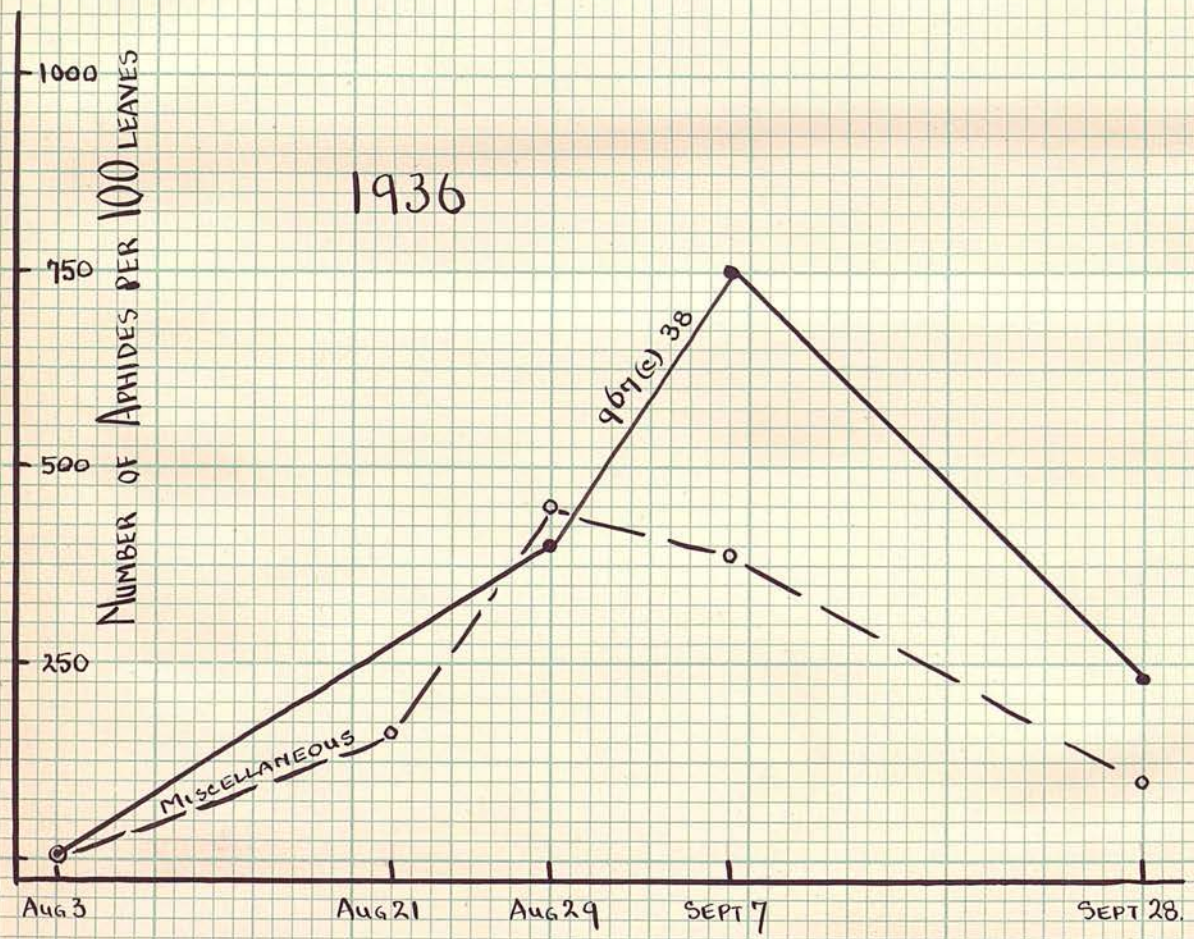

FIGURE 4. SEASONAL VARIATIONS IN THE APHIS POPULATIONS OF TWO POTATO CROPS AT AINVILLE, KIRKNEWTON, MIDLOTHIAN.

The sole point of difference is to be found in the relative sizes of the populations at each centre. In this connection a comparison of the data for 967 (c) 38 in Table 2, with those for the same variety in Table 1, shows clearly that on comparable dates the numbers of aphides per 100 leaves was markedly lower at Ainville. This difference may be ascribed to a smaller and probably a later initial infestation at the latter centre.

The varietal differences between 967 (c)38 and the miscellaneous seedlings are again well marked and thus provide supporting evidence of a biotic relationship between plant and insect which is particularly favourable in 967 (c) 38.

TABLE 2

AINVILLE

DATE	No. of Aphides per 100 leaves		% infested leaves	
1936	MISC.	967(c)38	MISC.	967(c) 38
Aug. 3	0	3	0	3
21	165	-	44	-
29	454	394	66	60
Sep. 7	392	756	84	94
28	96	230	54	74

DISCUSSION

The significant features of this preliminary survey are the predominance of Myzus persicae and the low initial and late maximum infestations of aphides which have been recorded in each year and at each centre. DAVIES (1934) has found an initial infestation in July of less than 20 aphides per 100 leaves to be indication of a negligible amount of virus ~~in~~ infection entering a crop through overwintered infective aphides. It may be concluded, therefore, that at each of the centres examined the introduction of viruses by migrant aphides reaching the crop in early summer was of very small proportion. There are, however, two further factors related to aphis development and distribution which have a bearing on dissemination of disease. Firstly, infection may spread internally from infector sources within a crop through multiplication and movement of aphides. This aspect of virus spread has been followed in some detail by periodic examination of the material contained in the susceptibility trials described in Section 3. It will be recalled that in these trials the diseased plants serving as sources of infection were numerous and uniformly distributed throughout the plots/

plots. By reason of the low initial infestation of aphides and also of the absence of disease during the early stages of growth, the dissemination of viruses within the crop may be ascribed entirely to the spread of infection from these sources.

TABLE 3

DATA FROM Y VIRUS PLOTS 1935-36

Date	No. Infected		Increase in Infection			
	No.	%	No	As % Total	As % Uninfected	Aphides
Jul. 5 1935	0	0	0	0	0	Few
Aug. 8 1935	84	16.3	84	16.3	16.3	Increasing
Aug. 23 1935	233	45.2	149	28.9	34.6	Numerous
Sept. 15 1935	362	70.2	129	25.0	43.6	Post-maximum
July 3 1936	427	82.8	65	12.6	42.5	-

The data from the Y virus trial of 1935 are given in Table 3. Clearly from this Table the spread of virus Y under the conditions of the trial was closely linked with the increase in aphis population and August and September were the critical months for the spread of infection within the crop. Furthermore, if the increase in infection is expressed as a percentage of the number of plants uninfected/

uninfected at the previous inspection, it will be seen that the relative increase was greatest during the period of maximum aphis populations.

The spread of leaf roll in 1935 occurred to a much smaller extent than that of virus Y and, at the time of the final inspection on September 15th, the amount of visible infection had reached only 3.1% of the total number of seedlings in the trial as compared with 70.2% in the virus Y trial. A further 29.8% of the seedlings were found in the following year to have contracted leaf roll, however, and the respective totals for the two trials were 82.8% for virus Y and 32.9% for leaf roll. Both trials contained identical plants and since the insect vectors of both viruses are the same, namely Myzus persicae, then the figure for virus Y infection may be taken as a minimum index of susceptibility to the act of infection. The same figure may also be taken as a minimum index of the susceptibility of the seedlings to the pathogen, virus Y. Controlled infection with the leaf roll virus proved that at least 68% of the seedlings were susceptible to this virus and, therefore, the differences in time and extent of spread between the two viruses cannot be explained on a basis of varietal differences affecting the relative susceptibilities of the material to either the act of infection/

infection or to the pathogens. The differences must be sought in some factor affecting the biotic relationship between plant and vector. It has already been observed that as between experimental crops the aphis population was lower and reached a maximum later in Field A which contained the leaf roll trial. It would seem therefore that with equality in other directions the amount of virus spread within a potato crop is related directly to the size of the aphis population.

The second factor affecting dissemination of viruses concerns the possibility that infection may be carried outwith a diseased crop by winged aphides receiving infection in the course of their development during the summer. The appearance of alatae in mid-August is very suggestive that such a possibility is not remote. Supporting evidence of spread of disease in this manner is forthcoming by the appearance, in plots well isolated from infector sources, of diseased plants which, from the time of symptom expression, have been judged to have become infected late in the season.

If a conclusion may be drawn from these various observations it is that in areas similar to those surveyed, and there is reason to believe that a greater part of Scotland differs from these areas in/

in degree only, dissemination of virus diseases is due more probably to spread of infection within a crop than to introduction of disease from external sources. This latter factor cannot be ignored entirely, however, but it would seem more probable that viruses are introduced during the latter part of the growing season than in the early summer.

SUMMARY.

1. A two year survey of aphis species and their distribution has been made.

2. Myzus persicae, SULZ. was found to be the predominating species in both years and at each of the centres investigated.

3. The initial infestation of potatoes with aphides appeared to be complete in July and of small proportions. In spite of the low initial infestation, however, a continuous multiplication of aphides during August led to high maximum infestations in late August and early September. It is concluded that under the conditions obtaining at the centres investigated the spread of virus diseases is due more probably to the spread of infection within the crop than to the introduction of viruses from external sources. Where this latter does take place it is ascribed to the migration of infective aphides in late summer.

4. The spread of virus diseases in experimental plots containing an efficient number of infector sources was found to bear a relation to the size of the aphis population and to be greatest in extent during the period of maximum infestation.

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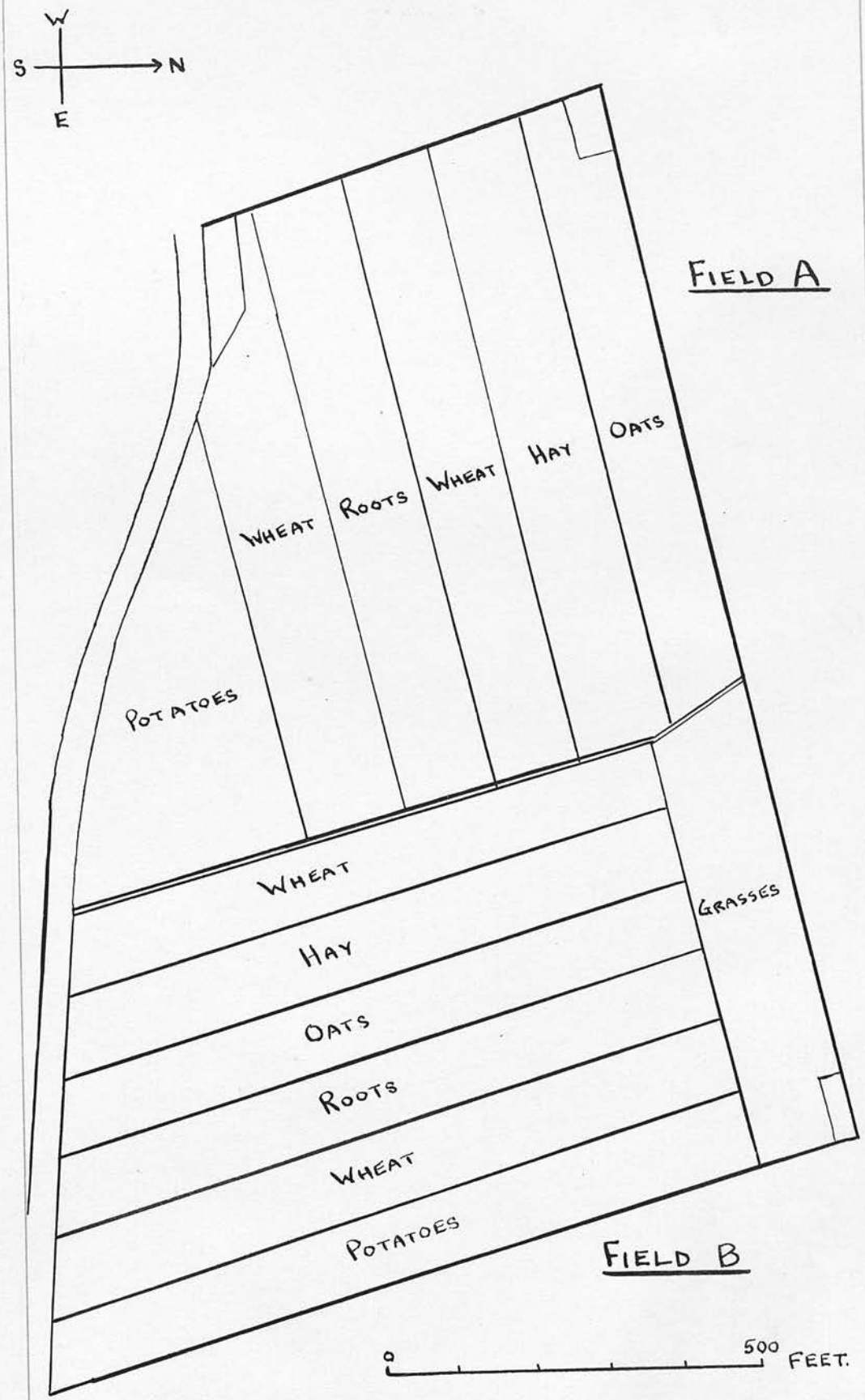
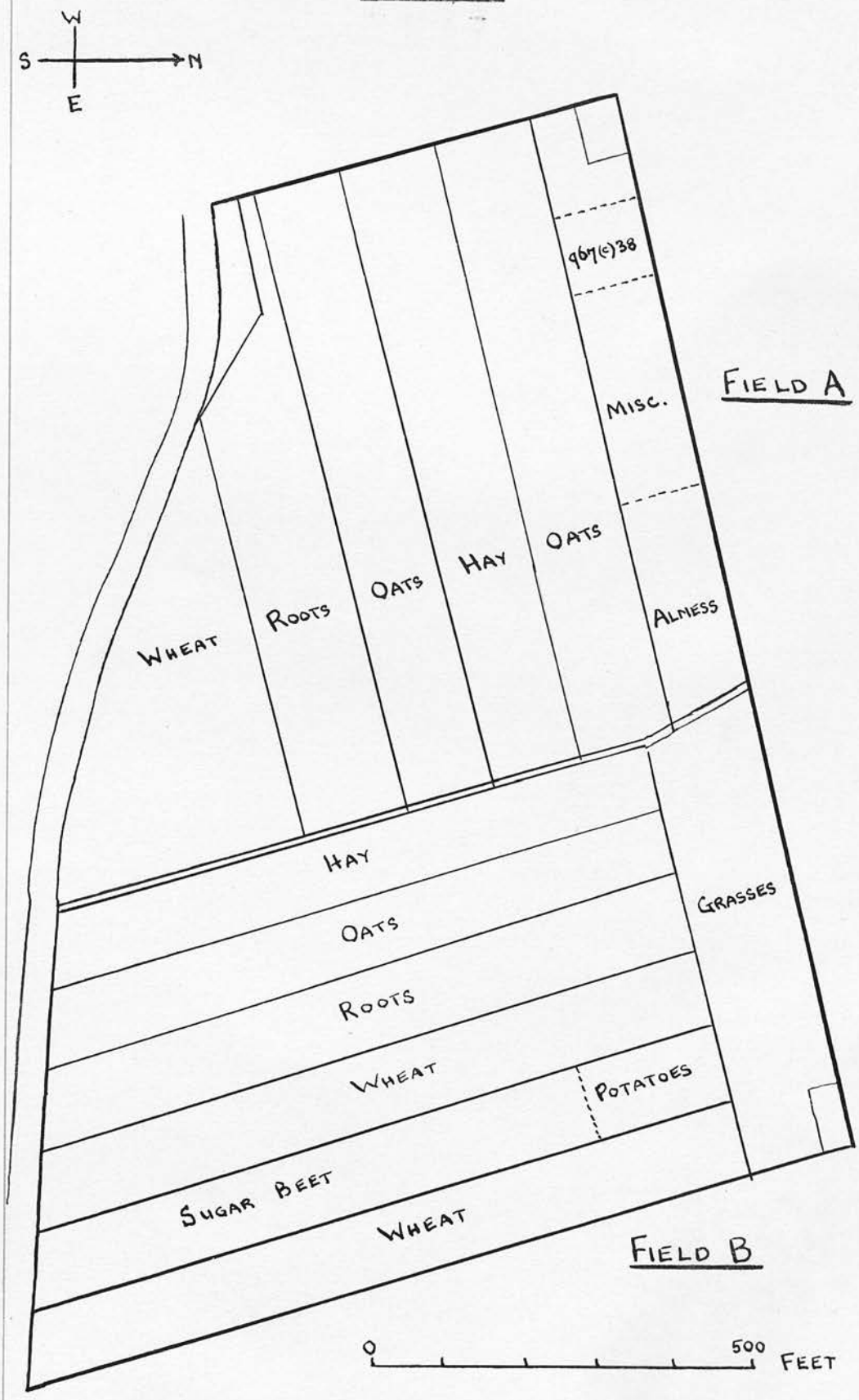
FIGURE 1.



Sketch plan of Fields A and B at the Plant Breeding Station, Corstorphine, showing situation of potato plots in 1935.

FIGURE 2.



Sketch plan of Fields A and B at the Plant Breeding Station, Corstorphine, showing situation of potato plots in 1936.

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